Assembly and Annotation of Sequences Surrounding the S locus in Primula vulgaris

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Since Clusius first documented floral heteromorphy in *Primula* in the 16th century, the genus has been a model system for those studying the development of different floral morphs on plants of the same species. Over the centuries, eminent botanist and geneticists, including Darwin, Hildebrand and Ernst, have furthered our understanding of the phenomenon in a number of species. In *Primula vulgaris* (Common Primrose), in which flowers take either a long styled (Pin) or short-styled (Thrum) form, heteromorphy is linked to a sporophytic self-incompatibility system, with both mechanisms under the control of the highly conserved, diallelic *Self-Incompatibility* (*S*) locus.

Whilst classical genetic approaches have identified basic functions of the *S* locus, as well as the order of the loci controlling these features within the locus, the molecular structure of this important region of the genome remains unknown. Recently, a number of molecular *S*-linked markers have been characterised, providing an opportunity to begin molecular characterisation of the locus as well as its immediate surroundings.

Using these markers as a guide, a single contiguous sequence has been assembled to join three of these markers together, spanning the region in which the mechanisms preventing recombination within the locus breaks down. Within this region, 51 genes have been identified and annotated. Homologues of these genes have been identified in *Solanum lycopersicum*, *Oryza sativa* and *Arabidopsis thaliana*, providing an insight into the convergence and divergence of genes between the four species.

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ABBREVIATIONS

Standard one letter abbreviations for amino acds and SI units are used along with the following abbreviations

aa	**Amino acids**
DMF	**Dimethylformamide**
EDTA	**Ethylenediaminetetraacetic Acid**
FDD	**Fluorescent Differential Display**
GSI	**Gametophytic Self-Incompatibility**
IPTG	**Isopropylthiogalactoside**
M-MLV	**Moloney Murine Leukaemia Virus**
PCR	**Polymerase Chain Reaction**
RACE	**Rapid Amplification of cDNA Ends**
RAPD	**Random Amplified Polymorphic DNA**
RFLP	**Restriction Fragment Length Polymorphism**
RT-PCR	**Reverse Trasncriptase PCR**
S-RNase	**Secreted RNase**
SCAR	**Sequenced Characterised Amplified Region**
SEM	**Scanning Electron Microscope**
SI	**Self-Incompatibility**
SSI	**Sporophytic Self-Incompatibility**
TBE	**Tris-borate-EDTA**
UTR	**Untranslated Region**
WT	**Wild Type**
X-Gal	**5-bromo-4-chloro-3-indolyl-β-D=galactosidase**

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CHAPTER ONE

INTRODUCTION

1.1 Overview

As hermaphrodites, the majority of angiosperm species possess both male and female reproductive organs within their flowers. Therefore, in order to avoid self-fertilisation and inbreeding depression, many hermaphrodite angiosperms have developed a wide variety of reproductive mechanisms that can help to promote outcrossing and limit self-fertilisation (Muller, 1932, Solbrig, 1976; Charlesworth and Charlesworth, 1987; Barrett, 2002a).

One of the most important methods of promoting outcrossing is self-incompatibility; the ability a flower to reject its own pollen (de Nettancourt, 2001). In the majority of species which display self-incompatibility, this is controlled by a single, multi-allelic locus known as the *Self-Incompatibility* (*S*) locus (Takayama and Isogai, 2005).

An alternative, and sometimes secondary, method of promoting outcrossing is the development of morphological differences between individuals, known as heteromorphy. The *Primula* genus is a classic example of this strategy and, with over 90% heterostylous species, has the largest number of heteromorphic species of any genus (Ganders, 1979; Lewis, 1979; Richards, 1986). The flowers of *Primula* can take one of two forms, named Pin and Thrum according to their outward appearance. In Pin individuals, the stigma atop the long style appears as a pin head within the mouth of the corolla while, in Thrum individuals, the ring of anthers around the corolla is said to look like the end of weaver's threads (Darwin, 1877). The flowers on any one individual always take the same form and this is closely linked to self-

incompatibility, with both mechanisms controlled by the *S* locus (Dowrick, 1956; Clapham, 1971).

Since Clusius first recorded two forms of flowers within *Primula* in 1583 (van Dijk, 1943, Ganders, 1979), many others, including Darwin (1862, 1877), Hildebrand (1863), Bateson and Gregory (1905), Mather and de Winton (1941), Dowrick (1956) and Charlesworth and Charlesworth (1979a) have taken steps to help further the understanding how this mechanism is inherited by *Primula* species. However, whilst the phenotypic and genetic characterisation of floral heteromorphy has received a great deal of attention, it is only recently that more has been paid to the molecular characterisation of this region (Manfield *et al*.; 2005, McCubbin *et al*.; 2006, Li *et al*., 2007, 2008, 2010, 2011).

A number of *S* locus markers have now been characterised in *Primula vulgaris* (Manfield *et* al., 2005; Li *et al., 2007, 2010)*. Using these markers as a guide, it is now possible to illuminate the area immediately surrounding the *S* locus and to identify other genes within this critical region of the *Primula vulgaris* genome.

1.2 Self-Incompatibility systems in *angiosperms*

Self-Incompatibility (SI) has been noted in over 100 species of flowering plant, with an estimated 40% of all angiosperm species able to prevent self-fertilisation (Igic *et al*., 2008). Although various SI systems have evolved independently in different species, most rely on a single *self-incompatibility* (*S*) locus, a complex inherited as a single segregating unit (Takyama and Isogai, 2005).

The *S* locus also displays a high level of allelic diversity with up to 145 different alleles estimated to exist within a single population of some species, giving rise to a

variety of possible SI phenotypes in pollen (Xue *et al*., 1996; Lawrence, 2000). As such, it is these SI phenotypes, expressed by pollen, and the passage of information between haploid pollen and diploid style, through male and female determinants, that form the basis of self-incompatibility (Golz *et al*., 1995).

When compatible pollen lands on the pistil, the dehydrated grain is able to absorb water from the style and resume metabolism, extruding the pollen tube to transmit genetic information to the ovary (Gaude and McCormick, 1999). However, in self-incompatible species, the style or stigma is able to reject incompatible pollen if the self-incompatibility phenotype of the pollen matches that of the style (Silva and Goring 2001). This SI phenotype can be determined by one of two genetic mechanisms, giving rise to two distinct SI systems: Gametophyic self-incompatibility (GSI) and Sporophytic self-incompatibility (SSI).

1.2.1 Gametophytic self-incompatibility

The most widespread form of SI is Gametophytic self-incompatibility (Newbign *et al*., 1993). In this system, compatibility between pollen and style is determined by the *S* allele contained in the haploid genome of pollen (Brewbaker, 1957). If the single *S* allele expressed by the gametophyte matches either of the co-dominant alleles possessed by the diploid style, the pollen is incompatible and the fertilisation process is arrested (Matton *et al*., 1994). In most GSI systems, this is not an immediate process. The incompatible pollen is allowed to germinate on the stigma, extruding a pollen tube into the style. Tube growth is then stopped as it grows through the central transmitting tract towards the ovary (Newbigin *et al.*, 1993).

Two types of GSI system have been described (Kao and Tsukamoto, 2004). The first of these is observed in the *Solanaceae, Rosaceae* and *Plantaginaceae* and relies on

secreted ribonuclease (S-RNase) as a female determinant, that is the component of the SI system produced by the female organs (Hiscock and McInnis, 2003a). In this system, a build up of S-RNase occurs within the transmitting tract of the recipient style, acting as a female determinant (McClure *et al.,* 1989). Upon extrusion of the pollen tube through the tract, the accumulated enzymatic S-RNase has been shown to degrade rRNA within the tube, unless the pollen inhibits it, though the precise mechanism of inhibition remains unknown (Luu *et al*., 2000). In addition to the S-RNase produced by the stlye, the male determinant in this GSI system has been shown to be an F-box protein encoded within the *S* locus. Again, the way in which this F-box protein interacts with the S-RNase remains unclear though the action of an F-box protein as a determinant suggests the involvement of the Ubiquitin-26S-proteasome degradation pathway (Sijacic *et al.,* 2004; Takayama and Isogai, 2005; Iwano and Takayama, 2012). A similar, S-RNase based system is also involved in the rejection of pollen from other species, making the S-RNase based system the most widely used pollen rejection system among angiosperms (McClure, 2004; Murfett *et al*., 1996).

The second type of GSI system has been be characterised exclusively in the *Papaveraceae,* and has been studied extensively in the field poppy, *Papaver rhoeas*. Although incompatibility in this system is also determined by the haploid genome of the pollen, this system differs largely from that seen in *Solanaceae, Rosaceae* and *Plantagenaceae* (Takayama and Isogai, 2005).

In *P. Rhoeas,* the female determinant has been characterised as a small (~15kDa) S protein named *P. Rhoeas* stigma *S* determinant (*PrsS*) that is secreted onto the stigma (Franklin-Tong and Franklin, 2003). Following pollination, this interacts with the highly polymorphic ~20kDa *P. Rhoeas* pollen *S* determinant (*PrpS*) protein that

acts as the male determinant (Wheel *et* al., 2009). Located in the plasma membrane of the pollen surface, *PrpS* interacts directly with PrsS to instigate a Ca^{2+} dependent phosphorylation of pyrophosphataes arrests pollen tube growth. Subsequently, a Ca^{2+} influx in the arrested pollen tube initiates programmed cell death and actin depolymerisation, thus preventing fertilisation (Hearn *et al.*, 1996; Huang *et al.*, 2004; Thomas and Franklin-Tong, 2004; de Graaf *et* al., 2006; Wheeler *et al*., 2009; Iwano and Takayama, 2012; Eaves *et* al., 2014). As such, this mechanisms also differs from that described above as the SI reaction occurs on the stigmatic surface, instead of within the central transmitting tract of the style (Hiscock and McInnis, 2003a).

1.2.2 Sporophytic self-incompatibility

Sporophytic self-incompatibility (SSI) differs from GSI in that the SI phenotype of the pollen is determined by the diploid genome of its sporophyte parent as opposed to its own haploid genome (Takayama and Isogai, 2005). As such, pollen grains appear to express two SI alleles, and rejection occurs if either allele matches those possessed by the style. In this system dominant-recessive relationships may occur between alleles independently in pollen and in the stigma (Matton *et al.*, 1994; Hiscock and McIInis, 2003b). SSI has been identified in a number of species and evidence suggests that it has evolved independently on each occasion, however many systems share the characteristic that pollen tube growth is arrested at an early stage (Ebert *et al*., 1989; Barrett, 1998).

1.2.2.i Sporophytic self-incompatibility in *Brassicaceae*

Of the various SSI systems used by different species, the most extensively studied system is that seen in the *Brassicaceae* (Hiscock and McInnis , 2003b). Similar to the GSI system seen in *Papaveraceae*, SSI in *Brassica* takes place on the stigmatic surface and is the result of protein interactions (Newbigin *et al.*, 1993). Although the *Brassica S* locus has been shown to contain as many as 17 genes, only 2 highly polymorphic genes are directly involved in the self-incompatibility reaction (Suzuki *et al*., 1999; Hiscock and McInnis, 2003b).

In this system, the female determinant, encoded by the *S* locus, is a serine/threonine receptor kinase named *S* locus receptor kinase (SRK) (Takasaki *et al*. 2000; Iwano and Takayama, 2012). Although able to function alone, the efficiency of SRK in rejecting incompatible pollen is enhanced by the action of a glycoprotein named *S* locus glycoprotein (SLG) (Takasaki *et al.*, 2000).

The male determinant in this system is a small, S locus cysteine-rich protein (SCR), also known as *S* locus protein 11 (SP11) (Schopfer *et* al., 1999; Shiba *et al*., 2001; Takayama *et al.*, 2001) SP11 is expressed in the anther of the parent plant and accumulates within the pollen coat (Suzuki *et al*., 1999). Upon pollination, SP11 in the pollen coat binds to SRK on the stigmatic surface, inducing autophosphorylation of SRK. The precise pathway leading to pollen rejection is still unclear but a number of proteins involved in the process have been identified. Following this activation of SRK, a complex is formed between SRK and *Brassica M* locus Protein Kinase (MLPK), activating downstream signalling proteins (Murase *et al*., 2004; Kakita *et al*., 2007a,b; Haasen and Goring, 2010). The best known of these downstream proteins is the *Brassica* ARM-Repeat Containing-1 (ARC1) protein, a Ubiquitin E3 ligase that Ubiquitinates a further protein Exo70A1, preventing secretory vesicles

from reaching the pollination site and the pollen is rejected (Gu *et al*., 1998; Samuel *et al*., 2009; Chapman and Goring, 2010; Indriolo and Goring, 2014). Support for the role of ARC1 in self-incompatibility has been provided by it absence in self-compatible *Brassica* species but presence in other species such as *Arabidopsis lyrata* (Indriolo *et al*., 2012). In the event of a match between *S* phenotypes of pollen and style, determined by allele of SP11 expressed in the pollen coat, the pollen is rejected. Interestingly, it has been shown that this mechanism can be reversed if pollen is transferred to a compatible stigma at an early stage of germination (Sarker *et al*., 1988).

1.2.2.ii Self-incompatibility in *Primula vulgaris*

In contrast to the well studies mechanism seen in *Brassicaceae*, the self-incompatibility system employed by the *Primulaceae,* in particular *Primula vulgaris*, is largely unknown. Unlike the homomorphic systems discussed above, *Primula vulgaris* is a heteromorphic species. As a result, it is difficult to compare self-incompatibility in *Primula* with the homomorphic GSI and SSI mechanisms described above. However, as a heteromorphic species, *Primula* is considered to possess a sporophytic self-incompatibilty system, as the pollen also displays dis[lays behavious determined by the diploid parent. This assumption has been supported by evidence from *Primula obconica,* where it has been demonstrated that materials from the anther are present within the pollen coat (Stevens and Murray, 1981; Gibbs, 1986; Charlesworth, 1988). This was also supported an earlier suggestion that pollen size and the male *S* phenotype in *Primula* were closely linked, indicating that the male determinant was determined by the diploid parent (Dulberger, 1975).

Beyond this, the precise mechanisms of the sporophytic self-incompatibility reaction in *Primula vulgaris* remains unclear, though it is known to be controlled by the same supergene as floral heteromorphy (Stevens and Murray, 1981). However, whilst other SSI systems have been characterised, the diversity of these, as a result of their independent evolutions, suggests that the mechanism seen in *Primula* will be largely unique (Barrett, 1998)

1.3 Characteristics of floral heteromorphy

Floral heteromorphy, the development of more than one form of flower in individuals of the same species, is a long studied phenomenon of flowering plants. A particularly well studied form of floral heteromorphy is heterostyly, Since it's first documentation by Clusius in 1581, at least 28, diverse angiosperm families have been reported in which flowers take different forms (van Dijk, 1943; Ganders, 1979; Barrett, 2002a; Kohn and Barrett, 1992; Mast and Conti, 2006). The condition was studied extensively by Charles Darwin, who first identified the variation in forms of flowers as a mechanism to promote outcrossing rather than a mere morphological oddity (Darwin, 1877; Barrett *et al*., 2000).

Heterostyly is a condition in which flowers from different individuals of the same species take different forms by altering the position of the male anthers and female style within the flower (Barrett, 2002a). This spatial separation of reproductive organs within the flower is known as herkogamy and is separate to dichogamy, a temporal separation in activity of reproductive organs, though both achieve the same goal of preventing sef-pollination (Webb and Lloyd, 1986; Lloyd and Webb, 1986). In many of the species identified as heterostylous, this arrangement of sexual organs

is linked to a diallelic, heteromorphic sporophytic self-incompatibility system, though a small number of heterostylous species such as *Narcissus triandrus* and *Salvia brandegeei* have been shown to be self-compatible (Gibbs, 1986; Barrett *et al.*, 1997*;* Barrett *et al.*, 2000).

Heterostylous species can be classed as distylous or tristylous, according to the number of flower morphs seen within the species. In distyly, two arrangements of style and anthers are seen between morphs and in tristyly, three floral morphs are observed. These arrangements are typically reciprocal between morphs, see Figure 1.1, and, in many species, the forms are named Pin (long styled) and Thrum (short styled). The spatial separation of style and anthers acts to increase the precision of pollen transfer between morphs. For example, pollen from the short styled form is deposited upon the insect pollinators body in such a way that it contacts with the stigma of the long styled form (Barrett, 2002a). In addition to this reciprocal herkogamy, differences are also often seen between features such as stigmatic papillae and pollen size (Ganders, 197; Barrett, 1992; Barrett, 2002a). These polymorphisms also contribute to an intramorph self-incompatibility system, preventing fertilisation between two individuals that possess the same stylar arrangement (Barret, 2002).

Another form of reciprocal herkogamy, recorded in at least 10 angiosperm families, is enantiostyly, in which the female organs of the flower are deflected to one side, resulting in flowers that are mirror images of each other (Jesson, 2002; Jesson and Barrett, 2002a; Jesson *et al*., 2003).

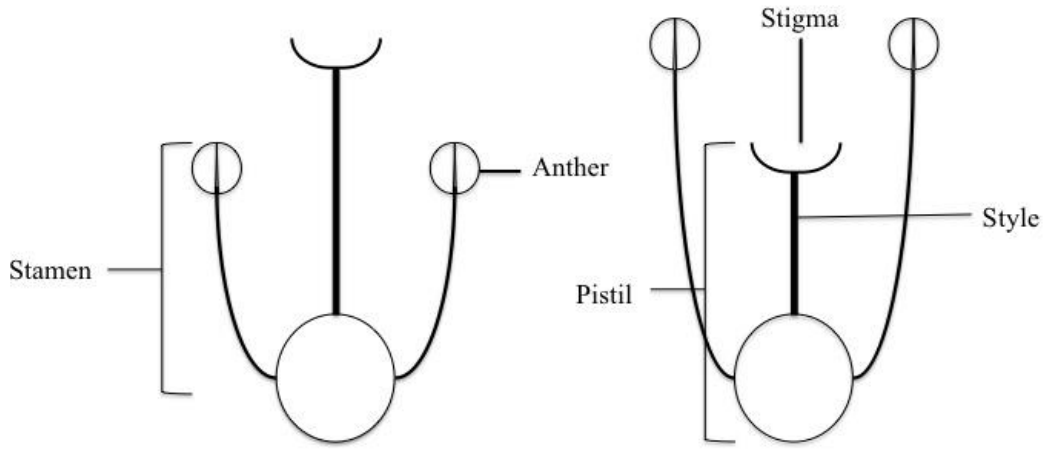

Figure 1.1 Reciprocal Herkogamy in distylous angiosperms. The anthers of the long styled (Pin) form (left) are level with the stigma of the short styled (Thrum) form (right) so as to increase the precision of intramorph pollination.

This has a similar effect on pollination as distyly described above, ensuring that pollen deposited on the right hand side of the pollinator comes into contact with the stigma of the mirror image morph (Bowers, 1975). There are two known types of enatntiostyly; monomorphic enantiostyly and dimorphic enantiostyly. In monomorphic individuals, flowers with styles deflected both left and right are present. However, in dimorphic enantiostyly, all flowers on an individual possess styles deflected in the same direction (Barrett, 2002b).

A further form of heteromorphy, called Flexistyly, has been documented more recently in tropical ginger species such as *Alpinia* (Li *et al*., 2001; Zhang *et al*., 2003). In these species, which produce up to 10 hermaphroditic flowers that last only a single day, two phenotypes are seen, in which the styles are extended at different angles. However, after midday, the styles extend downwards to expose anthers and the flower enters a male phase (Li *et al*., 2001). This form of heterostyly has been

named heterodichogamy, as it involves multiple style morphs present at different times and the morphs are often seen in a 1:1 ratio (Renner, 2001).

1.4 Floral heteromorphy and di-allelic self-incompatibility

As described in 1.3, floral heteromorphy is often closely linked to a diallelic self-incompatibility system and is therefore under the control of the *S* locus. Although this link was first recognised by Darwin (1862), it was Bateson and Gregory (1905) who demonstrated that the system was controlled by a single Mendelian dominance relationship. In almost all heteromorphic species, Pin individuals were shown to homozygous for this locus, with the genotype *ss*, whilst Thrum individuals are heterozygous, *Ss*. The genotype *SS* would also be phenotypically Thrum, though this genotype is extremely rare in nature (Vuilleumier, 1967). Subsequent genetic analysis has shown that this locus in fact consist of at least three separate functions that combine to govern self-incompatibility and floral heteromorphy and these will be described further in 1.5.2.

Floral heteromorphy and its link to self-incompatibility have been studied in a number of species including *Turnera*, *Fagopyrum* and *Linum* and these systems will now be examined more closely.

1.4.1 Floral heteromorphy in *Turnera*

Floral heteromorphy has been reported in 37 *Turnera* species though the most extensive studies have been made in *Turnera subulata* (White Alder) or *Turnera ulmifolia* (Yellow Alder) (Urban, 1883; East, 1940; Barrett, 1978).

The majority of *Turnera* populations are dimorphic, with flowers typical of either a long styled Pin morph and a short styled Thrum morph present in a 1:1 ratio (Barrett, 1978). The two morphs are incompatible and evidence suggests that distyly in this species evolved as a result of an already existent self-incompatibility between individuals (Martin, 1965).

Following the identification of a revertant short styled mutant, a genetic map of the *Turnera S* locus has now been initated (Tamari *et al*., 2005; Shore *et al.,* 2006). As such, 2 *S* locus markers have now been identified as well as 3 additional markers that co-segregatae with the locus (Labonne *et al*., 2008). A number of BAC contigs have also been assembled to span the *S* locus, allowing an estimation of recombination rates around the *S* locus and it is hoped that this will lead to the identification of the genes within the locus (Labonne and Shore, 2011).

In addition to these studies of distylous *Turnera*, monomorphic *Turnera* populations have also been identified, in which both long stamens and long styles are observed in self-compatible flowers (Barrett and Shore, 1987). Analysis of these populations as well as mutants generated using X-ray mutagenesis of *Turnera subulata* have shown that the *Turnera S* locus is very similar to the system seen in *Primula*, discussed in 1.5 (Labonne *et al.,* 2010). Typical of heteromorphic species, short styled individuals are heterozygous at the *S* locus (*Ss*) whilst long styled individuals are homozygous. However, although homozygous *SS* genotypes rarely occur in nature, *SS* individuals have been observed (Shore *et al*., 2006). This suggests that, although rare, homozygous Thrum individuals are viable and do not possess the *S* locus linked recessive lethal gene postulated in exist in other heteromorphic species such as *Primula* (Kurian and Richards, 1997; Shore *et al*., 2006).

1.4.2 Floral heteromorphy in *Fagopyrum*

Fagopyrum esculentum (buckwheat) is another example of a distylous angiosperm, with flowers again taking either a long styled (Pin) or short styled (Thrum) form and demonstrating distylous sporophytic self-incompatibility and a ratio between morphs of 1:1 is typically seen in populations (Cawoy *et al*., 2009).

The *S* locus of *Fagopyrum* is thought to contain 5 genes controlling style length (G), stylar incompatibility (I^s), pollen incompatibility (I^p), pollen size (P) and anther height (A) (Sharma and Boyes, 1961). As a result, the *S* and *s* alleles can be expanded and defined as GI^sI^pPA and gi^si^pa respectively, with Thrum individuals possessing the genotype GI^sI^pPA/ gi^si^pa whilst Pin individuals are gi^si^pa/ gi^si^pa (Sharma and Boyes, 1961; Cawoy *et al*., 2009). However, in homomorphic *Fagopyrum homotropicum*, an extra allele of the *S* locus has been identified, in addition to *S* and *s*, and has been named S^h (Woo *et al*., 1999).

Analysis of this allele, through interspecific crosses between *F. homotropicum* and *F. esculentum*, has shown that this allele retains a degree of control over heteromorphic self-incompatibility, suggesting that S^h is a result of recombination within the *S* locus (Matsui *et al*., 2003). This discovery has led to the suggestion that the control of floral heteromorphy and self-incompatbility, whilst linked, is split between two loci in *F. homotropicum*. The first locus is responsible for self-incompatibility, with a dominance relationship between alleles of $S>S^h>s$ and the second is responsible for flower morphology (Woo *et al*., 1999; Matsui *et al*., 2004; Wang *et al*., 2005; Cawoy *et al*., 2009).

The mechanism of self-incompatibility in *Fagopyrum* has also been observed. Following pollination with incompatible pollen, the pollen is allowed to germinate on the stigmatic surface and the pollen tube is extruded. Similar to the GSI system

seen in the *Solanaceae*, pollen tube growth is then arrested within the style, though Si in *Fagopyrum* is sporophyically controlled (Marshall. 1969). This inhibition of growth occurs closer to the stigma in Thrum individuals, though this results in the arrest of pollen tube growth at the same distance from the ovary in both forms (Cawoy *et al*., 2009; Schoch-Bodmer, 1934). Different proteins have been identified in short styled and long styled forms that are though to have a role in SI, including a 50kDa protein expressed in the Pin style 2 hours after fertilisation with incompatible pollen (Miljuš-Đukić *et al*., 2004). In addition to this, it has been shown the protein phosphatases and calcium are both involved in SI signal transduction (Miljuš-Đukić *et al*., 2003).

1.4.3 Floral heteromorphy in *Linum grandiflorum*

Similar to *Turnera* and *Fagopyrum,* two forms of *Linum grandiflorum* (Scarlet Flax) exist, possessing either a long or short style. However, unlike those species discussed above, little difference is seen in the height of the anthers between the flowers of the two morphs. As such, *L. grandiflorum* can be more accurately described as exhibiting stylar length polymorphism rather than being typically distylous, as used to describe *Turnera, Fagopyrum* and *Primula* (Lewis, 1943). Although the species lacks true reciprocal herkogamy, it can still be considered heterostylous and Darwin's studies of the species showed that the morphs are self-incompatible (Darwin, 1863, 1877; Weller, 2009).

In *L. grandiflorum,* pollination by incompatible pollen leads to different responses according to the nature of the pollen. When pollen from a long styled (Pin) individual lands on another Pin style, it is unable to germinate, as it is unable to absorb water from the style for rehydration, In contrast, when pollen from a short

styled individual (Thrum) lands on another Thrum style, rehydration occurs and the pollen tube is extruded, though this later bursts within the style (Lewis, 1943). Similar to the case seen in *Fagopyrum*, although this termination of pollen tube growth within the style is typical of a GSI system, SI in *Linum* is sprophyticaly controlled (Gibbs, 1986). This is possibly due to the difference is stigmatic seen between the two forms using SEM analysis. Through studies of a number of species which display SSI, Heslop-Harrison and Shivanna (1977) characterised the 'wet' and 'dry' types of stigma. In the Pin form of *L. grandiflorum*, the stigma is coated in a smooth pellicle, typical of the 'dry' type of stigma. In contrast, the Thrum stigma is of the 'wet' type, having a disrupted, broken coating with fluid secreted onto it (Heslop-Harrison and Shivanna, 1977; Ghosh and Shivanna, 1980). Additionally, upon hydration of pollen grains, proteins on the pollen surface, and originating from the parent anther, are unfolded and emitted onto the stigmatic surface (Dulberger, 1990). Therefore, whilst homozygous *ss* Pin pollen is immediately recognised as incompatible, this may explain why germination of heterozygous *Ss* Thrum pollen is not immediately prevented.

A further difference between the two forms of *L. grandiflorum* is the osmotic pressure observed in pollen and styles. In both compatible pollinations (Pin pollen to Thrum style or Thrum pollen to Pin style) the same ration of 4:1 exists in the osmotic pressure of pollen:style. However, in intramorph pollinations, this ratio is 5:2 in Pin and 7:1 in Thrum. As such, it has been proposed that this ratio has a direct effect on the successful growth of pollen tubes, though more recent studies have been unable to provide evidence to support this intriguing suggestion (Lewis, 1943, Murray, 1986).

1.5 Floral heteromorphy in *Primulaceae*

1.5.1 Phenotypic characterisation of heteromorphy

Primula species have been model systems for the study of heteromorphy since Clusius documented the different forms of flowers in *Primula* species (van Dijk, 1943, Ganders, 1979). However, the most influential work on the phenotypic characterisation of hetermorphy was Charles Darwin's work in 1862 (Darwin, 1862). It was in this work that Darwin combined existing horticultural knowledge of hetermorphy with his own studies of heterostyly and he later drew his ideas together in his 1877 work *The Different Forms of Flowers on Plants of the Same Species*. Although he also published works on other heteromorphic species such as *Linum*, the first chapter of this book focuses solely on the *Primulaceae*, with particular emphasis on *P. veris* (Cowslip), and his work formed a basis for much future work on the system (Darwin, 1862, 1863, 1877; Weller, 2009).

When studying *P. veris*, Darwin (1877) observed that the pistil in a Pin flower was almost exactly twice the length of that seen in a Thrum flower. In Pin flowers, the stigma can be seen in the corolla mouth and sometimes extends out above the petals and the surface of the stigma bears a small depression. Conversely, the stigma in Thrum flowers is more rounded and, in its place, a ring of anthers can be seen around the mouth of the corolla. However, the shape of the corolla is more cylindrical in Thrum flowers, whilst a widening of the tube is seen in Pin flowers. Darwin (1877) also noted that the stigmatic papillae cells in Thrum were a half to a third of the size of those seen in the rougher stigma of Pin flowers.

In his examinations of the flowers' male organs, Darwin (1877) recorded that, unlike some other heteromorphic species, the anthers were the same size in both forms. However, the pollen that Darwin collected from Pin flowers was only 2/3 the size of

that which he collected from Thrum flowers. Further to this, the Pin pollen that Darwin observed had an oblong shape, in contrast to the rounded shape of Thrum pollen.

Darwin (1862, 1877) also conducted a number of crosses between Pin and Thrum individuals to observe the pattern of self-incompatibility within *Primula veris*, terming crosses between morphs 'legitimate unions' and referring to those between the same forms as 'illegitimate unions.' This led to a further observation that, although Pin flowers possessed a larger ovule than Thrum flowers, they produced fewer seeds following a legitimate union.

Through these experiments, Darwin demonstrated that, although illegitimate unions did lead to seed set, the amount of seeds produced was much smaller than that seen in legitimate unions. The seeds produced through illegitimate unions were also less viable than those produced legitimately and seed set following illegitimate unions was severely restricted in conditions that had no effect on seeds produced legitimately. Darwin also recorded that, of the different illegitimate unions possible, self-fertilisation produced fewer seeds than cross fertilisation between two individuals of the same morph, concluding that the self-fertilisation of a Thrum individual produced the fewest seeds of all.

Darwin (1877) also recorded his observations of *P. vulgaris* (common primrose). Similar to *P. veris*, he noted that *P. vulgaris* Thrum pollen is larger than that seen in Pin and concluded that the Thrum form, again, was the most fertile of the two forms.

Despite its status as a model species for the study of heteromorphy, homomorphic populations of *P. vulgaris* are known to exist (Crosby 1940, 1949). Crosby (1940) described flowers, collected from a *P. vulgaris*, population in Somerset that possessed high anthers, as seen in Thrum, in addition to a long style, as seen in Pin.

In addition to this, the stigma possessed long papillae, characteristic of Pin individuals (Crosby, 1940; Darwin, 1877). Crosby (1940, 1949) suggested that these 'Long Homostyle' individuals should be self-fertile, since they possess both Thrum type pollen and a Pin type stigma. He also argued that the dynamics of a population containing Long Homostyle individuals would be affected by the viability of any self-fertilised individuals. If the self-fertilised individuals were less viable than cross-fertilised individuals, the trait should be removed from the population if 'normal' Thrums are present. However, if the homozygotes were more viable than heterozygotes, the population should contain only Long Homostyle individuals. A third scenario exists, in which populations would consist of Pin and Long Homostyle individuals, with the Thrum form absent and it is this third scenario that is observed (Crosby 1940, 1949). Through counts of the population recorded in Somerset, as well as a second population recorded in the Chiltern hills, Crosby observed that the Long Homostyle condition spreads throughout a mixed Pin and Thrum population until an equilibrium state is reached. In this state, roughly 20% of a population will be of the Pin form and 80% will be Long Homostyles, whilst the Thrum form will be lost as a result of its (Crosby 1949). Crosby suggested that the reason for this loss of Thrum forms was a competitive disadvantage in Thrum pollen when compared to the pollen produced by Long Homostyles, which could be used in self-pollination. However, the rise in proportion of Long Homostyles within a heterostylous population was explained in two ways (Charlesworth and Charlesworth, 1979b). Whilst, Crosby (1958) suggested that the capacity of Long Homostyles for self-fertilisation led to the rapid increase in numbers within a population, Bodmer (1958) attributed this to an increased viability in cross-fertilisation between Long Homostyle individuals. Bodmer (1960) later showed that whilst self-fertilisation

within a population does occur, a subsequent reduction in homozygote viability promotes the cross-fertilisation model.

Short Homostyle individuals have also been observed in which a shortened, Thrum type style is seen alongside the lower anther position seen in Pin individuals (Ganders, 1979, Li *et al.*, submitted). However, investigations into population dynamics of Short Homostyle individuals have shown that the condition is less likely to become established within a population due to the recessive nature of many Short Homostyle characteristics (Dowrick, 1956, Charlesworth and Charlesworth 1979b). As a result, this form of *Primula* has been less well studied than the Long Homostyle form.

Figure 1.2 The Pin and Thrum forms of *Primula vulgaris*. a). The outer view of a Pin flower. b). The positions of anthers and style in a Pin flower. c). The outer view of a Thrum flower. d). The positions of anthers and style in a Thrum flower.

1.5.2 Genetic characterisation of heteromorphy

Following Darwin's observation on the phenotypic differences between the Pin and Thrum forms of *Primula* species, subsequent work focussed on the genetic characterisation of heteromorphy within the genus.

The first work to demonstrate the inheritance pattern of heteromorphy in *Primula* was completed by Bateson and Gregory (1905). Through cross-pollination of both forms of *Primula sinensis* and *Primula acaulis* individuals, in addition to crosses between homostyled individuals, Bateson and Gregory provided evidence to support the existing hypothesis that heteromorphy was subject to a Mendelian inheritance pattern, with the Thrum allele dominant to Pin (Bateson and Gregory, 1905).

Following the establishment of this dominance relationship, Ernst (1933, 1936a, 1936b, 1955) conducted a number of experiments using homostylous and self-fertile *Primula* species such as *Primula viscosa* and *Primula hortensis* (Dowrick 1956). Following a number of crosses between individuals, Ernst (1933, 1936b) identified progeny in which specific characteristics, such as style length, had recombined, separating the characteristics usually inherited collectively. Using this data, Dowrick (1956) identified three genetically distinct characteristics, controlled by separate loci within the *S* locus. The first of these, termed *G*, controlled the length of the style and stigmatic papillae, as well as the female determinants of the self-incompatibility reaction. The second characteristic identified was the height of the anthers within the flower, termed *A*. The final locus, termed *P*, controls the male determinant of the self-incompatibility reaction as well as the size of pollen grains (Dowrick, 1956). Although Ernst had proposed that the separation observed between these characteristics was a result of a mutation of the *S* locus as whole, Dowrick argued that the order of the three loci within the *S* complex was important and that

recombination between the *G, A* and *P*, loci that led to this separation of characteristics. Dowrick used Ernst's data to postulate different recombination scenarios that could lead to the separation of characteristics recorded by Ernst, finally proposing the order *GPA* as the most likely sequence of loci within the locus (Dowrik, 1956). The Thrum characteristics observed in *Primula* were shown to be dominant for all three loci and, as such, the Thrum allele was subsequently characterised as *GPA* whilst the recessive Pin allele was denoted *gpa*. It was known, following Bateson and Gregory's (1905) work, that Thrum individuals were heterozygous, and, therefore, were assigned the genotype *GPA/gpa* whilst homozygous Pin individuals possessed the genotype *gpa/gpa*.

It has already been discussed (see 1.4) that floral heteromorphy is often tightly linked to diallelic self-incompatibility. As such, the two alleles of the *S* locus in *Primula* are often referred to as *GPA* or *gpa*, as opposed to *S* or *s*, and this notation can be used to characterise the actions of the different alleles. Due to the shortened length of styles in Thrum individuals, it can be concluded that the dominant *G* allele supresses the long style encoded by *g* whilst *A* raises the height of the anthers from that caused by *a*. Similarly, *P* leads to a larger pollen size than *p.* SEM analysis of style and anther cells has revealed that, whilst the lengthening of the style caused by *g* is a result of increased cell elongation, the change in anther height produced by *A* is a result of increased cell division (Webster and Gilmartin, 2006).

As discussed in 1.5.1, homostyled individuals have been recorded in *Primula vulgaris* and these characteristics can be described by recombination between the *G, P* and *A* functions. Homostyle individuals typically arise through a recombination event between the *G* and *P* loci, producing gametes with the genotypes *Gpa* or *gPA.* Long Homostyle individuals can therefore arise through the fertilisation of a Pin

(*gpa*) gamates with the recombined *gPA* gamete, producing the phenotype *gPA/gpa*. The resultant offspring possesses the lengthened style typical of Pin individuals but retains the larger pollen and high anthers of a Thrum flower. Conversely, fertilisation by a *Gpa* gamete would produce the genotype *Gpa/gpa*. The resultant offspring would therefore possess the supressed style of a Thrum flower, alongside the small pollen and low anthers typically seen in Pin (Manfield *et al*., 2005).

Recent work has expanded further on these 3 loci. These have included the suggestion of a lethal gene linked to the Thrum allele as well as a separation between the incompatibility reactions and the style/anther phenotypes controlled by *G* and *A.* As such, it has now been proposed that up to 7 genes may exist within the *S* locus (Kurian and Richards, 1997).

1.5.3 Evolution of heteromorphy in *Primulaceae*

Two models have been proposed for the evolution of heterostyly (Mast and Conti, 2006). The first of these, proposed by Charlesworth and Charlesworth (1979a), proposes that two self-incompatible phenotypes developed within a homomorphic species, with reciprocal herkogamy developing subsequent to this. The alternative model, first proposed by Darwin (1877), proposes that reciprocal herkogamy developed within a population in which elongated styles were already present (Mast and Conti, 2006).

Mather (1950) supported the second of these routes, reasoning that an existing background genotype produced a coordinated complex of characteristics that developed into the heterostyly we are familiar with today. This has been further supported by evidence from the *Primula* subgenus *Sphondylia*, in which many species show varying degrees of heteromorphy. Comparison of the varying degrees

of distyly and self-incompatibility seen in the species of this subgenus suggests the existence of an ancestral homomorphic species that developed herkogamy before intra-morph incompatibility (Al Wadi and Richards, 1993). However, this evidence is largely speculative and the precise method by which heteromorphy evolved in *Primulaceae* remains uncertain.

1.6 *S* locus-linked floral mutations of *Primula vulgaris*

Floral mutations, phenotypes that differ from the known wild type, have been observed and cultivated for over two thousand years. Floral mutations such as doubles, in which a flower develops a greater number of petals than usual, have been recorded in roses since the time of Pliny, in the 1st century, and, before then, Theophrastus before 256 BC (Meyerowitz *et al*., 1989). Double mutations are a type of homeotic mutation, a common form of mutation in which one type of floral organ develops in the place usually occupied by others (see Meyerowitz *et al*., 1989 and Theißen, 2001 for reviews). Homeotic mutations can be explained by the ABC model, in which the four whorls of the flower a determined by the functions of three classes of genes (Coen and Meyerowitz, 1991). The outer whorl of the flower, which typically contains sepals, is determined by the lone function of A function genes whereas the second whorl, containing petals, results from the interaction of A function and B function genes. B function genes also interact with C function genes to form stamens and anthers in the third whorl whilst the innermost whorl, containing the carpel, is the result of C function activity (Coen and Meyerowitz, 1991). These A, B and C function genes are typically MADS box transcription factors (Ng and Yanofsky, 2001).

Although much of the scientific attention on *Primula* has focussed on floral heteromorphy and self-incompatibility, a number of floral mutations have also been characterised. These include *double,* in which petals or stamens may form in the place of carpels, *Jack in Green*, which develops leaf-like sepals and *split perianth*, in which the petals and sepals fail to fuse correctly (Webster and Gilmartin, 2003).

Three further floral mutations are *Hose in Hose, sepaloid* and *oakleaf*. These three mutations are of particular interest as they are linked to the *S* locus, with each mutation typically co-segregating with either the Pin or Thrum allele, and will now be examined more closely.

1.6.1 *Hose in Hose*

The *Hose in Hose* mutation in *P. vulgaris*, in which sepals are converted into petals, has been documented and studied since the 16th century (Gerard, 1597; Webster and Gilmartin, 2003). The phenotype, shown in Figure 1.3, which has the appearance of one flower growing out from another, is dominant to the wild type form and it has been demonstrated that the locus responsible for the mutation, discussed below in 1.7.3, is linked to the *S* locus, with almost all *Hose in Hose* individuals presented the low stigma and high anthers typical of Thrum individuals (Ernst, 1931; Webster and Grant, 1990; Webster and Gilmartin, 2003). However, whilst the *Hose* in Hose mutation was originally thought to co-segregate with the Thrum allele only, Pin individuals have also now been identified. This suggests that rare recombination events may occur between the two loci and a linkage distance of 0.7 cM has been estimated between *S* and *Hose in Hose* (Webster and Grant, 1990; Webster and Gilmartin, 2003; Li *et al*. 2010).

Figure 1.3 The *Hose in Hose* mutation in *Primula vulgaris*. The sepals of the *Hose in Hose* phentotype undergo homeotic conversion to petals

Figure 1.4 The *sepaloid* mutation in *Primula vulgaris*. The petals of the *sepaloid* phentotype undergo homeotic conversion to sepals.

Additionally, *Hose in Hose* mutants are known to display differing severities of mutation, with some individuals showing only partial conversion of sepals to petals. Full reversion of petalloid sepals to wild type sepals has also been observed (Webster and Gilmartin, 2003). Conversion of sepals to petals in this way is typical of an ectopic expression of B gene function in the first whorl of the flower. As a result of this increased level of expression, both A and B functions combine to produce petals, as would typically be seen in the second whorl of the flower (Coen and Meyerowitz, 1991; Li *et al.* 2008, 2009).

SEM analysis of early stage *Hose in Hose* flowers has shown that the first developmental stages are similar to those seen in wild type. However, at the stage at which sepals would usually expand to cover the developing flower, thinner, broader petalloid sepals can be seen to develop. In instances of incomplete conversion, differences between wild type and *Hose in Hose* cannot be seen until a later point in the flowers development (Webster and Gilmartin, 2003).

1.6.2 *Sepaloid*

The *sepaloid* mutation in *P. vulgaris* is a more recent discovery than *Hose in Hose*, with the first examples identified among commercial primroses in 1996 (Webster and Gilmartin, 2003). In the *sepaloid* mutation, petals undergo homeotic conversion to sepals, typical of a loss of B function genes. In the absence of the B function, the A function genes are expressed alone in the second whorl, leading to the development of sepals in place of petals (Li *et al*., 2008). Similar to the *Hose in Hose* mutation, the *sepaloid* phenotype displays variability in its severity. Whilst some individuals develop sepals in the 1st and 2nd whorls only, more severe instances have been observed. The instances include the conversion of the 3rd whorl to sepals

surrounding functional or non-functional carpels and even the complete conversion of all four whorls to sepals (Webster and Gilmartin, 2003, Li *et al*., 2008). As such, not all *sepaloid* individuals are fertile. Analysis of the *sepaloid* phenotype has demonstrated that it is a recessive mutation that typically co-segregates with the Pin allele of the *S* locus, with a suggested linkage distance of 0.3 cM between the two (Webster and Gilmartin, 2003; Webster, 2005). The suggested position of *sepaloid* relative to the *S* locus and other genetic markers can be seen in Figure 1.5.

SEM analysis of developing *sepaloid* flowers has shown that no differences can be observed between developing *sepaloid* and wild type flowers until the development of whorls 1 and 2. At this stage, *sepaloid* flowers begin to develop a deep hollow in the centre of the flower and the development of flower primordial is retarded in comparison to wild type flowers. In contrast to the defined rings of organs seen in wild type flowers, the floral organs of *sepaloid* flowers remain joined to form a spiral and the innermost tissue that would form the carpel may be absent (Webster and Gilmartin, 2003).

1.6.3 *Oakleaf*

Similar to the *sepaloid* phenotype, the *S* linked *Oakleaf* phenotype was characterised relatively recently, and a population was establish following the identification of a single individuals in 1999. Unlike *Hose in Hose* and *sepaloid*, the *Oakleaf* phenotype affects both flowers and leaves, with leaves developing lobes similar to those seen in *Quercus*. *Oakleaf* individuals typically develop flowers with split calyces. The *Oakleaf* phenotype is dominant to wild type and, as is seen in *Hose in Hose* and *sepaloid*, the severity of the phenotype varies between individual (Webster, 2005).

The phenotype described above is typical of an overexpression of Class I *KNOX* homeodomain transcription factors (Lincoln *et al*., 1994; Chuck *et al*., 1996; Hay and Tsiantis, 2006). However, transcriptomic analysis of *Oakleaf* individuals has shown that no Class I *KNOX*-like genes (termed Class 1 *PvKNOX*) are up regulated in *Oakleaf* individuals. Whilst Class I *PvKNOX* candidates have now been discounted, other candidates remain. Similar to the *sepaloid* mutation, *Oakleaf* typically co-segregates with the Pin allele of the *S* locus and has a suggested linkage distance of 11.5 cM (Cocker *et al*., submitted). The suggested position of *Oakleaf* relative to the *S* locus and other genetic markers can be seen in Figure 1.5.

1.7 Characterisation of *Primula vulgaris S* locus markers

Whilst both the phenotypic and classical genetic basis of the heteromorphy in *Primula* are well understood, it is only much more recently that work has begun to focus on the molecular characterisation of the condition. As a result, the molecular structure of the *S* locus remains largely unknown (Manfield *et al*., 2005). However, if the *S* locus can be sequenced and annotated, this would not only elucidate the loci controlling heteromorphic self-incompatibility in *Primula*, but would also serve as a gateway to access and analyse the downstream signalling pathway that underlies heteromorphy and self-incompatibility. Additionally, it may be possible to gain insights into the evolution of the heteromorphy within *Primula*, allowing for comparisons with other species that independently evolved a similar system (Manfield *et al.,* 2005; McCubbin *et al*., 2006).

By using the extensive, historical information available on heteromorphy in *Primula,* as well as the known *S* linked floral mutations discussed in 1.6, Manfield *et al.* (2005) initiated the molecular characterisation of the *S* locus by identifying genetic

markers linked to the locus. To date, four markers have been characterised and will now be discussed in more detail.

1.7.1 PvSLP1

The first *S* locus marker to be characterised was a restriction fragment length polymorphism (RFLP) marker identified in the Blue Jeans cultivar of *Primula vulgaris*, and named *P. vulgaris S* linked polymorphism 1 (PvSLP1) (Manfield *et al*., 2005). By using RAPD-PCR to amplify both Pin and Thrum genomic DNA, a 323bp product was observed that could only be amplified from Thrum DNA. This RAPD sequence was converted into a Sequence-Characterised Amplified Region (SCAR) marker and used as a probe in a genomic Southern blot analysis. Following hybridisation to Pin and Thrum DNA, two Thrum specific bands were identified, suggesting that the SCAR marker corresponded to an RFLP marker that was duplicated in Thrum individuals (Manfield *et al*., 2005).

Once identified as a Thrum-specific marker, this RFLP sequence was used to screen a *P. vulgaris* var. Blue Jeans phage λ library and an 8.8kb genomic DNA sequences containing the RFLP marker was constructed (Pavlov, 1997; Manfield *et al*., 2005). In addition to this, PCR amplification of *PvSLP1* from homostylous individuals, which have undergone recombination within the *S* locus, suggests that the marker resides on the *A* side of the locus. The suggested position of PvSLP1 relative to the *S* locus and other genetic markers can be seen in Figure 1.5.

Further analysis of this assembled genomic fragment indicated homology to Ty3/*gypsy*-like retrotransposon sequences as well as the presence of multiple short, repetitive sequences, similar to those seen surrounding the *S* locus of other genera

such as *Petunia* and *Papaver* (Coleman and Kao, 1992; Wheeler *et al*., 2003; Manfield *et al*., 2005).

1.8.2 *PvSLL1* and *PvSLL2*

Although the identification of PvSLP1 provided the first molecular marker linked to the *S* locus in *P. vulgaris,* it represented a polymorphic non-coding region of the genome (Li *et al*., 2007). As such, it was desirable to identify new *S* locus linked markers that were also expressed genes and, in 2007, Li *et al* were successful in identifying two genes in *P. vulgaris* var. Blue Jeans that possessed different Pin and Thrum alleles (Li *et* al., 2007).

In order to identify genes that showed differential expression between Pin and Thrum flowers, Fluorescent Differential Display (FDD) (Kuno *et al*., 2000) using RNA from developing flowers was used. A total of 19 genes were identified that were reliably amplified differentially from Pin and Thrum RNA, 10 of which were Thrum specific and 9 were Pin specific. However, RT-PCR and northern analysis were only able to reproduce this evidence of differential expression for 1 of these 19 genes. As such, an alternative method of Southern analysis was used to demonstrate linkage between these 19 genes and the *S* locus. Of these 19, 2 genes produced RFLPs between Pin and Thrum genomic DNA, suggesting linkage to the *S* locus. These two genes were subsequently named *P. vulgaris S locus linked 1* and 2 (*PvSLL1* and *PvSLL2*) (Li *et al*., 2007).

Further Southern analysis of *PvSLL1* and *PvSLL2* demonstrated that three alleles of each gene exist, 2 of which are coupled to the Pin allele (*PvSLL1/2*^{P1} and *PvSLL1/2*^{P2}) of the *S* locus and 1 to Thrum (*PvSLL1/2*^{T}*)*. Pin individuals may be heterozygous or homozygous for the Pin alleles of *PvSLL1* and *PvSLL2* whilst

Thrum individuals are heterozygous, with at least one allele of each gene being the Thrum allele. Comparison with *Arabidopsis* genomic databases suggested that *PvSLL1* encodes a small transmembrane protein whilst *PvSLL2* encodes a *CONSTANS-LIKE* protein (Li *et al*., 2007).

Controlled crosses were performed and, following the analysis of F_1 and F_2 plants, no recombinants were detected for *PvSLL1*. As such, it was suggested that a genetic distance of < 0.57 cM existed between *PvSLL1* and the *S* locus. Conversely, a single recombinant for *PvSLL2*, a Pin individual possessing the $PvSLL2^T$ allele, was observed in the F_1generation. In an F_2 population of 146 progeny, a further 2 recombinants were also detected, suggesting a distance of 1.37 cM between *PvSLL2* and the *S* locus. In addition to this, further analysis of *PvSLL1* and *PvSLL2* in recombinant Short and Long Homostyles demonstrated that *PvSLL1* and *PvSLL2* are located on opposite sides of the *S* locus. The presence of $PvSLL1^T$ within Long Homostyles suggests that the gene maps to the *A* side of the locus as it has maintained its coupling with the dominant *P* and *A* alleles following recombination. Conversely, homozygosity for the Pin alleles of *PvSLL2* in Long Homostyles suggests that this gene maps to the *G* side of the locus (Li *et al*., 2007). The suggested positions of *PvSLL1* and *PvSLL2* relative to the *S* locus and other genetic markers can be seen in Figure 1.5.

1.8.3 *PvGLO*

In an attempt to characterise the gene responsible for the *sepaloid* mutation, described above in 1.6.2, two *Primula* B function genes were identified based on homology to the *Antirrhinum majus* B function genes *deficiens* (*def*) and *globosa* (*glo*) (Schwarz-Sommer, 1992; Tröbner *et al.,* 1992; Li *et al.,* 2008). In this study, it

was demonstrated that expression of both the *Primula DEFICIENS* homologue (*PvDEF*) and the *Primula GLOBOSA* homologue (*PvGLO*) were affected in the *sepaloid* mutant. It was shown that *PvDEF* is not linked to the *S* locus and, as such, could not be a candidate for *sepaloid*. However, *PvGLO*, which does show linkage, was investigated further (Li *et al*., 2008, 2010).

PvGLO was characterised by first using *Antirrhinum* cDNA probes to isolate partical cDNA clones in *P. vulgaris* var. Blue Jeans. 3' and 5' RACE were then used to obtain full-length cDNA clones. Three alleles of *PvGLO* were identified. Two of these alleles, $PvGLO^{P1}$ and $PvGLO^{P2}$ are specific to Pin individuals whilst Thrum flowers possess the $PvGLO^{T}$ allele. The discovery of this Thrum allele of *PvGLO* within a *seplaoid* individual therefore disqualified the gene as a *sepaloid* candidate since the phenotype is linked to the Pin allele of the *S* locus. Whilst the true identity of *sepaloid* remains unknown, evidence of recombination between the *sepaloid* and *PvGLO* suggests that the locus lies between *PvGLO* and the *S* locus (Li *et al*., 2008).

As discussed in 1.6.1, the *S* linked phenotype *Hose in Hose* is typical of an ectopic expression of a B-function gene and it has subsequently been shown that a retrotransposon insertion in *PvGLO* is responsible for this phenotype. Furthermore, due to its linkage with the *S* locus, *PvGLO* has now become the fourth known molecular marker for the *S* locus and the position of *PvGLO* relative to the *S* locus and other genetic markers can be seen in Figure 1.5. (Li *et al*., 2010).

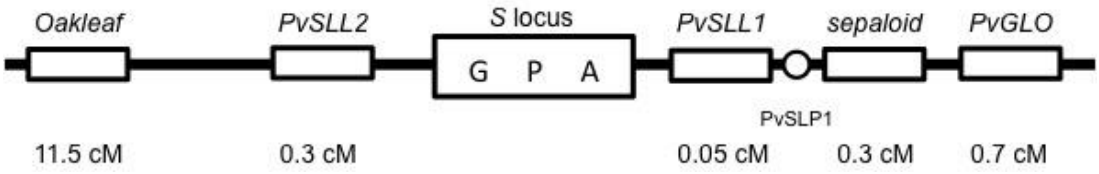

Figure 1.5: Summary map of the *S* locus and surrounding markers. Relative positions of *S* locus marker genes are represented by rectangles. The non-gene marker PvSLP1 is represented with circle. Linkage distances between each marker and the *S* locus are provided. Map is not drawn to scale.

1.8 Summary and project aims

The two forms of *Primula vulgaris* have been recorded in historical documents for hundreds of years, though it was Charles Darwin who first recognised the forms, their significance and their equal numbers within populations (Darwin, 1862, 1877; van Dijk, 1943). Since Darwin's seminal work, the genetic basis of the Pin and Thrum phenotypes seen in *Primula* species has been well characterised and is largely understood. However, through the recent identification of the *S* locus markers *PvSLP1*, *PVSLL1*, *PvSLL2* and *PvGLO*, the molecular characterisation of the *S* locus has begun to gather pace. Furthermore, the construction of a BAC library, cloned from sequences associated with the *S* locus in *P. vulgaris* var. Blue Jeans means that a significant resource for the molecular characterisation of the locus is now available (Li *et al*., 2011).

Whilst the identification and characterisation of these markers has allowed for increased scrutiny of the *S* locus itself, the area immediately surrounding the locus is still largely ignored. Using the known *S* locus markers described above to probe the library, a number of BACs have been identified in the areas flanking the locus. By performing BAC walks, it has also now been shown that *PvSLL1, PvSLP1* and

PvGLO are located together on the *A* side of the locus, whilst *PvSLL2* is located on the *G* side (Li *et al*., submitted).

Analysis of *PvSLL1* has demonstrated that it is strongly linked to the Thrum allele of the *S* locus. In contrast to this, *PvGLO*, and its mutant phenotype *Hose in Hose*, are known to recombine with the *S* locus (Li *et al*., 2010). This suggests that, although the mechanism that limits recombination within the *S* locus prevents recombination between *S* and *PvSLL1*, this mechanism breaks down between *PvSLL1* and *PvGLO*. Furthermore, the strong linkage observed between *PvSLP1* and *S* (Manfield *et al*., 2005) suggests that this degeneration occurs between *PvSLP1* and *PvGLO*.

As work continues to characterise the molecular structure of the *S* locus itself, this project will supplement this work and will have the following aims:

- To assemble a single, contiguous sequence that connects the two genetic markers *PvSLP1* and *PvGLO* through the use of existing BAC DNA sequence data. This sequence can then extended to incorporate the genetic marker *PvSLL1*, providing a physical link between *PvGLO* and the boundary of the *S* locus itself.
- To annotate this sequence in order to identify all of the genes between the *S* locus and *PvGLO*. In addition to providing an insight into the nature of the genes immediately surrounding the *S* locus, it is also hoped that the gene responsible for the *sepaloid* mutation, described in 1.6.2 and thought to be located within this region, will be identified.
- To use the above annotations as a means of examining synteny between *Primula vulgaris* and other plant species in the hope of determining whether the genes found in this region pre-date the arrival of the key *S* locus genes.

CHAPTER TWO

Materials and Methods

2.1 Materials and Suppliers

2.1.1. General Suppliers

Agilent technologies (www.agilent.com) 5301 Stevens Creek Blvd. Santa Clara, CA 95051. USA: Stratagene XL-1 Blue Competent Cells.

Epicentre (www.epibio.com) 5602 Research Park Blvd., Suite 200, Madison, WI. 53719 USA: BACMAX DNA Purification Kit, Riboshredder RNase Blend.

Eurofins MWG Operon (www.eurofinsgenomics.eu) Eurofins Genomics, Anzinger Str. 7a, 85560 Ebersberg. Germany: Primer production and DNA sequencing.

GE Healthcare (www.gehealthcare.com) Nightingales Lane, Chalfont St Giles, Buckinghamshire. HP8 4SP. UK: Nucleon Phytopure Genomic DNA Extraction Kit.

Life Technologies Ltd (www.lifetechnologies.com) 3 Fountain Drive, Inchinnan Business Park, Paisley. PA4 9RF. UK: Qubit Fluorimeter, RNAqueous RNA Isolation Kit, RNA*later* RNA stabilization solution, M-MLV Reverse Transcriptase Kit, RNaseOUT Recombinant Ribonuclease Inhibitor.

New England Biolabs (www.neb.uk.com) 75-77 Knowl Piece, Wilbury Way, Hitchin, Hertfordshire. SG4 0TY. UK: Phusion High-Fidelity DNA Polymerase, 100 bp DNA Ladder, 1 Kb DNA Ladder, Restriction Enzymes.

Promega (www.promega.com) Delta House, Southampton Science Park, Southampton. SO16 7NS. UK: RQ1 RNase-Free DNase, Go-Taq Flexi DNA Polymerase Kit, pGEM-T Easy Vector System, PureYield Plasmid Miniprep System.

Qiagen (www.qiagen.com) Qiagen House, Fleming Way, Crawley West, Sussex. RH10 9NQ. UK: QIAquick PCR Purification Kit, QIAquick Gel Extraction Kit.

Sigma-Aldrich (www.sigmaaldrich.com) Sigma-Aldrich Company Ltd., Dorset, England. UK: Media and Solutions.

Thermo Fisher Scientific Inc (www.thermofisher.com) 81 Wyman Street, Waltham, MA 02451. USA: Nanodrop ND-1000 Spectrophotometer, Long PCR Enzyme Mix,

2.1.2 Media and Solutions

Bacteriological growth media and stock solutions referred to in 2.2 were made as follows. Autoclave conditions used for sterilisation were 15 lb/sq.in for 20 minutes.

2.1.2.i Media

Luria Bertani (LB) Medium: 10 g Bacto-Tryptone, 5 g Bacto-Yeast Extract, 10 g NaCl in 1000 ml distilled water. pH7 with NaOH and autoclave

LB Agar Plates: 15 g Agar in 1000 ml LB Liquid Medium (pH7)

2.1.2.ii Solutions

Agarose Gel: Agarose dissolved in 400 ml 0.5xTBE. For 1% Agarose: 4 g. For 1.5% Agarose: 6 g. For 2% Agarose: 8g. Melt in microwave. Add 1 µl Ethidium Bromide per 50 ml gel.

Ampicillin Stock: 50 mg/ml in 50% Ethanol. Store at -20 °C. Working concentration 50 µg~100 µg/ml

Ethylenediamine Tetra Acetic Acid Disodium Salt Dihydrate (EDTA) (0.5 M): 186.1 g of EDTA.2H_2O in 1000 ml distilled water. pH8 with NaOH and autoclave

Ethidium Bromide Stock: 10 mg/ml. Store in dark at room temperature

Isopropylthio-β-D-galactoside (IPTG) Stock (20%): 2 g IPTG in 10 ml H_2O. Filter through 0.22 micron filter. Store at -20 °C

5x Tris-borate-EDTA (TBE): 54 g Tris base and 27.5 g boric acid to 20 ml 0.5M EDTA (pH8.0). Make up to 1 litre with disitilled water

5-Bromo-4-chloro-3-indolyl-β-D-galactoside (X-gal) (50 mg/ml): X-gal in dimethylformamide (DMF) Store at -20 °C in dark

2.1.3 Online Tools and Software

Chromas Lite: technelysium.co.au/?page_id=13

EMBL-EBI ClustalW2: www.ebi.ac.uk/tools/msa/clustalw2

ExPASy: www.expasy.org/tools

NCBI BLAST: blast.ncbi.nlm.nih.gov/Blast.cgi

Phytozome BLAST: www.phytozome.net

Primer3Plus: www.primer3plus.com

Sequence Manipulation Suite: www.bioinformatics.org/sms2

TAIR BLAST: www.arabidopsis.org/blast

2.1.14 Plant Material

Mature *Primula vulgaris* plants were maintained at the University of Durham Botanic Gardens and the University of East Anglia Plant Growth Facility. Plants were kept in greenhouses to protect them from weather conditions.

2.2 Methods

2.2.1 Nucleic Acid Extraction and Synthesis

2.2.1.i Genomic DNA Extraction

Extraction of genomic DNA from *Primula vulgaris* plant tissue was performed using the illustra Nucleon Phytopure Genomic DNA Extraction Kit (GE Healthcare). All volumes given are for extraction of DNA from 0.1g of plant tissue, typically young leaves. Volumes given in square brackets were used when 1g of starting tissue was used.

0.1g [1g] fresh weight of leaf tissue was frozen in liquid nitrogen and ground using a mortar and pestle to disrupt the cell walls. Once a free flowing powder was achieved, the tissue was transferred into a screw-capped tube suitable for centrifugation. To

initiate cell lysis, 600 µl [4.6 ml] of Reagent 1 (EDTA, Sodium Dodecyl Sulphate) was added to the tube. When RNA free DNA was required, RNase A was added to a concentration of 20 µg/ml and the sample was incubated at 37 °C for 30 minutes. Following this, 200 µl [1.5 ml] of Reagent 2 was added the sample was mixed to homogeneity and then incubated at 65 °C for 10 minutes with regular agitation. The sample was then placed on ice for 20 minutes. To extract DNA, 500 µl [2 ml] cold Chloroform (stored at -20 °C) was added followed by 100 µl [200 µl] of Nucleon Phytopure DNA Extraction Resin Suspension. The mixture was incubated at room temperature for 10 minutes with regular agitation and centrifuged at 1300 x *g* for 20 minutes, during which the resin formed a barrier between the upper DNA containing phase and the lower chloroform phase. The upper phase was removed, added to an equal volume of cold isopropanol (stored at -20°C) and mixed to precipitate the DNA. The precipitated DNA was pelleted by centrifugation at 3250 x *g* for 10 minutes and then washed with cold 70% Ethanol (stored at -20°C). The pelleted DNA was centrifuged again at 3250 x *g* for 10 minutes. Following centrifugation, the supernatant was discarded and the pellet was allowed to air-dry. Finally, the pellet was resuspended in TE Buffer. TE Buffer was added in 10 µl aliquots to ensure that the DNA was suspended in the minimum possible volume, providing the highest concentration possible. DNA concentration was measured using a Qubit Fluorimeter (Life Technologies).

2.2.1.ii RNA Extraction

Extraction of RNA from *Primula vulgaris* plant tissue was performed using the Ambion RNAqueous RNA Isolation Kit (Life Technologies). RNA is extracted from a variety of tissues including leaves, roots, flower buds and individual floral organs

dissected from flower buds. Leaf, root and flower bud tissues were frozen immediately either in liquid nitrogen or on dry ice. Individual floral organs were dissected under a microscope and stored in 5-10 volumes (w/v) RNA*later* RNA stabilization solution (Life Technologies) before being frozen in liquid nitrogen or on dry ice. All samples were weighed prior to freezing. Unless stated otherwise, all centrifugation steps took place at 13000 x *g* at room temperature.

Cell walls were disrupted by grinding the frozen tissue in liquid nitrogen using a pestle and mortar to yield a free flowing powder. The powdered tissue was transferred into screw-capped tube suitable for centrifugation containing 12 volumes (w/v) of Lysis/Binding Solution (formamide, formaldehyde) and 1 volume of Plant RNA Isolation Aid and mixed until homogeneity was achieved. When large tissue samples were used, the mixture was centrifuged for 3 minutes at 3250 x *g* to remove any large debris. An equal volume of 64% Ethanol was added to the mixture and a 700 µl aliquot was applied to a filter cartridge placed inside a collection tube. The RNA was bound to the filter cartridge by centrifugation. The flow-through was discarded and another 700 µl aliquot as applied to the filter. This was repeated until all of the lysate/ethanol mixture had been processed. If the volume lysate/ethanol mixture exceeded 2 ml, a new filter cartridge was used so as not to exceed RNA binding capacity. The bound RNA was then washed by applying 700 µl Wash Solution #1 (guanidinium thiocyanate) to filter catridge and centrifuging for 1 minute. The RNA was further washed with two 500 µl aliquots of Wash Solution #2/3 (100% Ethanol), drawn through the filter cartridge by centrifugation as before. Following the second wash, the empty filter cartridge was centrifuged for a further 30 seconds to remove residual ethanol. RNA was eluted from the filter by applying 50 µl of Elution Solution preheated to 75 °C and centrifuging for 30 seconds at room

temperature. A second elution was then performed using a further 20 µl Elution Solution. For larger samples, a third elution using 10 µl of Elution Solution was also performed. RNA concentration was measured using a Qubit Fluorimeter (Life Technologies).

2.2.1.iii First Strand cDNA Synthesis

Prior to first stand cDNA synthesis, RNA was digested using RQ1 RNase-Free DNase (Promega) to endonucleolytically remove residual double stranded and single stranded DNA. 1 µl RQ1 RNase-Free DNase 10X Reaction Buffer (400mM Tris-HCl, 100 mM $MgSO_4$, 10mM $CaCl_2$) was added to 1-8 µl RNA. RQ1 RNase-Free DNase was added in a ratio of 1 unit/µg RNA, giving a total final volume of 10 µl. The mixture was then incubated at 37 °C for 30 minutes. The digestion was stopped by the addition of 1 µl RQ1 DNase Stop Solution (20 mM Ethylene Glycol Tetraacetic Acid (EGTA)) and the DNase was inactivated by incubation of the mixture at 65 °C for 10 minutes. Following digestion, RNA concentration was measured again using a Qubit Fluorimeter (Life Technologies).

First strand cDNA was synthesized using Moloney Murine Leukemia Virus Reverse Transcrtiptase (M-MLV RT) according to the Invitrogen M-MLV Reverse Trasncriptase Kit protocol (Life Technologies). 1µl Oligo $(dT)_{12-18}$ primer was added to a tube containing 1 µg DNase treated RNA and 1 µl 10 mM dNTP Mix (10 mM each dATP, dGTP, dCTP and dTTP). Sterile H_2O was added to a total volume of 12 µl. The mixture was heated to 65 °C for 5 minutes and chilled quickly on ice. 4 µl 5X First Strand Buffer (250 mM Tris-HCl, 375 mM KCl, 15 mM $MgCl_2$) was added to the mixture along with 2 µl Dithiothreitol (DTT) and 1 µl (40 units) RNaseOUT Recombinant Ribonuclease Inhibitor (Life Technologies). The contents of the tube

were mixed gently by inversion at incubated at 37 °C for 2 minutes. 1 µl (200 units) M-MLV was added and the mixture was incubated at 37 °C for 50 minutes. The reverse transcription reaction was then terminated by heating the mixture to 70 °C for 15 minutes. Concentration of the synthesized cDNA was measured using a Qubit Fluorimeter (Life Technologies).

2.2.1.iv BAC DNA Extraction

BAC colonies were stored in glycerol at -80°C. Before extraction of BAC DNA could begin, colonies from the glycerol stock were grown in culture. Chloramphenicol was added to LB media in a 1:100 dilution, giving a final concentration of 12.5 µg/ml. Using a heat sealed micropipette tip, a BAC colony sample was pricked from the glycerol stock and added to a 1.5 ml microcentrifuge tube along with 1 ml of LB/antibiotic mixture. The tube was then incubated overnight (min. 16 hours) at 37 °C.

500 µl of overnight culture was added to 5 ml of LB/antibiotic was in a 50-ml screw-capped tube, with the cap taped lightly into place so as not to prevent air flow in and out of the tube. The liquid culture was incubated in a shaking incubator at 37 °C for 30 minutes, shaking at 220 rpm. Following this initial incubation, 5.5 µl induction solution was added, giving a 1:1000 dilution. The culture was incubated in a shaking incubator at 37 °C for a further 4 hours, shaking at 220 rpm.

BAC DNA was extracted from cells inn liquid culture using the BACMAX DNA Purification Kit (Epicentre). Before beginning the extraction procedure, BACMAX Solutions 1, 3 and 4 were chilled on ice, according to the protocol. 5.5 ml of liquid culture was transferred to a 15 ml screw-capped tube and centrifuged at 3250 x *g* for 3 minutes to pellet the cells. 200 µl of BACMAX Solution 1 was added to the pellet

and the tube was vortexed vigorously to resuspend the cells. Following resuspension, 400 µl of BACMAX Solution 2 was added to the cells and mixed gently by inversion to lyse the cells. 300 µl of BACMAX Solution 3 was added and the tube was again mixed gently by inversion until a white precipitate formed. The tube was then incubated on ice for 15 minutes and then centrifuged at 3250 x *g* for 15 minutes at 4 °C to remove any remaining cellular debris. The supernatant was transferred to a 1.5 ml microcentrifuge tube using a 1000 µl large orifice pipette tip to minimize the risk of shearing the DNA. 540µl of room temperature isopropanol was added to the supernatant and mixed by inversion to precipitate the DNA. The DNA was then pelleted by centrifugation at 3250 x *g* for 15 minutes at 4 °C and the isopropanol was carefully poured off. The pellet was allowed to air-dry at room temperature for 5 minutes and then resuspended in 250 µl TE Buffer by tapping and swirling the tube. Vortexing was avoided to prevent damage to the DNA. Any RNA suspended with the DNA was removed by adding 3 µl of RiboShredder RNase Blend (Epicentre) to the solution and incubating for 30 minutes at 37 °C. Following RNA digestion, the tube was cooled to room temperature and 250 µl of chilled BACMAX Solution 4 was added to the tube. The solutions were mixed thoroughly by tapping the tube and incubated on ice for 15 minutes. The tube was then centrifuged at 3250 x *g* for 15 minutes at 4°C and the supernatant was recovered and transferred to a fresh microcentrifuge tube. The recovered DNA was precipitated with 1 ml 100% Ethanol and pelleted by centrifugation at 3250 x *g* for 15 minutes at 4 °C. The Ethanol was removed and the pellet was allowed to air-dry at room temperature for 5 minutes. Finally, the DNA was resuspended in 25 µl of TE Buffer. DNA concentration was measured using a Qubit Fluorimeter (Life Technologies).

2.2.1.v Phenol/Chloroform extraction and ethanol precipitation of DNA

The following procedure was used to precipitate DNA from an existing solution. Equal volumes of phenol and chloroform were mixed and added in a 1:1 ration to a 1.5 ml microcentrifuge containing suspended DNA. If the volume of suspended DNA was low, H_2O was added to create a final volume of ~100 µl before the addition of Phenol/Chloroform. The solutions were mixed thoroughly by vortexing for 1 minute then centrifuged at 20,913 x *g* for 5 minutes. The upper aqueous phase was removed and added to a fresh microcentrifuge tube with an equal volume of chloroform. The mixture was vortexed for 1 minute and centrifuged for 5 minutes at 20,913 x *g* as before. The upper aqueous phased was removed, added to a fresh microcentrifuge tube and mixed with 3x volume of cold 100% Ethanol (stored at -20°C) to precipitate the DNA. The tube was then centrifuged for 20 minutes at 20,913 x *g* at 4°C to pellet the DNA. Following centrifugation, the ethanol was decanted and the pellet was washed with 300µl cold 70% Ethanol (stored at -20°C) and centrifuged for a further 5 minutes at 20,913 x *g* at 4°C. The ethanol was removed and the pellet allowed to air-dry and then resuspended in either sterile, RNA free H_2O or TE Buffer. DNA concentration was measured using a Qubit Fluorimeter (Life Technologies).

2.2.1.vi Nucleic Acid Quantitation

a) Nanodrop Spectrophotometer Quantitation

Spectrophotometric quantitation of nucleic acids was performed using a Nanodrop ND-1000 Spectrophotometer (Thermo Fisher Scientific Inc.). The spectrophotometer was initialized by pipetting 1.5 µl H_2O onto the lower pedestal of the Nanodrop and lowering the upper arm to form a column of liquid between the two pedestals.

Following initialization, the pedestals were cleaned with tissue and a blank measurement was made using 1.5 µl of the same medium that the nucleic acid to measured had been suspended in, typically H_2O, TE Buffer or Elution Buffer (containing 10 mM Tris.Cl pH8). The pedestals were cleaned again and 1.5 µl of the nucleic sample to be measured was loaded onto the lower pedestal and measured.

b) Qubit Fluorimeter Quantitation

Fluorometric quantitation of nucleic acids was performed using a Qubit2.0 Fluorometer (Life Technologies). The Qubit Working Solution was prepared by adding nµl of the necessary Qubit reagent (dsDNA, ssDNA or RNA) to n x 199 µl of the necessary Qubit buffer (dsDNA, ssDNA or RNA) where n = number of samples to be measured. Two standards were also prepared in order to calibrate the fluorometer. To prepare the standards, 190 µl Qubit Working Solution was added to two Qubit Assay Tubes containing Standard 1 and Standard 2 respectively. The standards were read successively by placing the assay tubes into the sample chamber of the fluorometer and measuring fluorescence. To prepare samples for measurement, 180-199 µl Qubit Working Solution was added to 1-20 µl of the sample to be measured to give a total volume of 200 µl. All tubes were mixed thoroughly and incubated at room temperature for 2 minutes. Sample concentrations were calculated by placing the assay tubes into the sample chamber of the fluorometer and measuring fluorescence. Stock concentrations were calculated based on the Sample:Qubit Working Solution ratio within the assay tube.

2.2.2 Polymerase Chain Reaction

All PCR reactions were performed using a Bio-Rad T100 Thermal Cycler or a Bio-Rad iCycler iQ Real Time PCR system.

2.2.2.i Primer Design and Synthesis

Oligonucleotide for all PCR reactions were designed using the Primer3Plus primer design tool (Primer3Plus). All primers were synthesized by Eurofins MWG Operon (Eurofins). Sequences and properties of all primers are detailed in Appendix A.

2.2.2.ii Standard PCR

a) Standard PCR for General Applications

For most PCR applications, the Go-Taq Flexi DNA Polymerase Kit (Promega) was used. This kit contains GoTaq DNA Polymerase, a nonrecombinant modified form of *Taq* DNA polymerase lacking 5' to 3' exonuclease activity. The volumes of reagents used in standard PCR reactions using Go-Taq Flexi DNA Polymerase are shown in Table 2.1. Most PCR reactions were performed in a total volume of 25 µl. A total volume of 50 µl was used when the products were to be isolated for use in other applications. Template DNA was typically added at an initial concentration of 20-100 ng/µl. All sets of PCR reactions contained a negative (template-free) control reaction to highlight any contamination of PCR reagents.

PCR Reagent	Volume in 25 µl Reaction	Volume in 50 µl Reaction
5X GoTaq Flexi Buffer	**5 µl**	**10 µl**
$MgCl_2$ Solution (25 mM)	**2 µl**	**4 µl**
dNTP Mix (10 mM each)	**0.5 µl**	**1 µl**
Forward Primer (10 pmol/µl)	**1 µl**	**2 µl**
Reverse Primer (10 pmol/µl)	**1 µl**	**2 µl**
Template DNA	**1 µl**	**2 µl**
GoTaq DNA Polymerase (5 u/µl)	**0.1 µl**	**0.2 µl**
H_2O	**14.4 µl**	**28.8 µl**
Total Volume	**25 µl**	**50 µl**

Table 2.1: Standard volumes of PCR reagents used in a reaction with GoTaq DNA Polymerase.

Table 2.2 describes the typical PCR conditions used with GoTaq DNA polymerase. The number of Denaturation-Annealing-Extension cycles was altered according to the concentration of DNA template used in the reaction and was often altered when trying to optimise the reaction. The length of the extension step was varied according to the predicted size of the product being amplified, allowing 1 minute of extension per Kilobase of product. The annealing temperature was also varied according to the melting temperatures of the oligonucleotide primers being used. This typically varied between 50°C and 60°C and was calculated based on the melting temperatures of the primers detailed in Appendix A. Pairs of primers were designed to have similar

melting temperatures and the annealing temperatures used were typically 2-3°C below these values. This was then raised to increase specificity of amplification.

Step	Temperature	Time	# Cycles
Initial Denaturation	**95°C**	**3 min**	**x1**
Denaturation	**95°C**	**30 sec**	**x35**
Annealing	**50°C - 60°C**	**30 sec**	
Extension	**72°C**	**1 min/kb**	
Final Extension	**72°C**	**5 min**	**x1**
Infinite Hold	**4°C**	∞	**x1**

Table 2.2: Standard conditions used for PCR with GoTaq DNA Polymerase.

Following PCR, products were either processed immediately or stored at 4°C until ready for use. For long term storage, products were frozen at -20°C.

b) Standard PCR with Proofreading

When PCR products were to be sequenced or used for other sequence specific applications, Phusion High-Fidelity DNA Polymerase (New England Biolabs), an alternative polymerase enzyme that also possessed proofreading functionality, was used. The volumes of reagents used in PCR reactions using Phusion High-Fidelity DNA Polymerase are shown in Table 2.3. PCR reactions could be performed in a total volume of 20 µl or 50 µl. However, as most applications that required proofreading also required purified PCR results, a reaction volume of 50µl was used when using this enzyme. Template DNA was typically added at an initial

concentration of 20-100 ng/µl. All sets of PCR reactions contained a negative (template-free) control reaction to highlight any contamination of PCR reagents.

PCR Reagent	**Volume in 20 µl Reaction**	**Volume in 50 µl Reaction**
5X Phusion HF Buffer	**4 µl**	**10 µl**
dNTP Mix (10 mM each)	**0.4 µl**	**1 µl**
Forward Primer (10 pmol/µl)	**1 µl**	**2.5 µl**
Reverse Primer (10 pmol/µl)	**1 µl**	**2.5 µl**
Template DNA	**1 µl**	**2.5 µl**
Phusion DNA Polymerase (2 u/µl)	**0.2 µl**	**0.5 µl**
H_2O	**12.4 µl**	**31 µl**
Total Volume	**20 µl**	**50 µl**

Table 2.3: Standard volumes of PCR reagents used in a reaction with Phusion DNA Polymerase.

Table 2.4 describes the typical PCR conditions used with Phusion DNA Polymerase (New England Biolabs). The number of Denaturation-Annealing-Extension cycles was altered according to the concentration of DNA template used in the reaction and was often altered when trying to optimise the reaction. The length of the extension step was varied according to the predicted size of the product being amplified, allowing 30 seconds of extension per Kilobase of product. The annealing temperature was also varied according to the melting temperatures of the

oligonucleotide primers being used. This typically varied between 50°C and 60°C and was calculated based on the melting temperatures of the primers detailed in Appendix A.

Step	**Temperature**	**Time**	**# Cycles**
Initial Denaturation	**98°C**	**30 sec**	**x1**
Denaturation	**98°C**	**10 sec**	**x35**
Annealing	**50°C - 60°C**	**30 sec**	
Extension	**72°C**	**30 sec/kb**	
Final Extension	**72°C**	**10 min**	**x1**
Infinite Hold	**4°C**	∞	**x1**

Table 2.4: Standard conditions used for PCR with Phusion DNA Polymerase.

Following PCR, products were either processed immediately or stored at 4°C until ready for use. For long term storage, products were frozen at -20°C.

2.2.2.iii Long PCR

For PCR applications where large regions of sequence beyond the amplification range of standard PCR enzymes were being amplified, Fermentas Long PCR Enzyme Mix (Thermo Fisher Scientific Inc.) was used. Fermentas Long PCR Enzyme Mix contains both Taq DNA Polymerase and a second thermostable DNA polymerase with proofreading activity and is able to amplify up to 21 kb from genomic DNA templates. The volumes of reagents used in Long PCR reactions using this mix are shown in Table 2.5. All PCR reactions were performed in a total

volume of 50 µl. Template DNA was typically added at an initial concentration of 20-100 ng/µl. All sets of PCR reactions contained a negative (template-free) control reaction to highlight any contamination of PCR reagents.

PCR Reagent	**Volume in 50 µl Reaction**
10X Long PCR Buffer with 15 mM $MgCl_2$	**5 µl**
dNTP Mix (2 mM each)	**5 µl**
Forward Primer (10 pmol/µl)	**2 µl**
Reverse Primer (10 pmol/µl)	**2 µl**
Template DNA	**2 µl**
Long PCR Enzyme Mix (5 u/µl)	**0.5 µl**
H_2O	**33.5 µl**
Total Volume	**50 µl**

Table 2.5: Standard volumes of PCR reagents used in a reaction with Fermentas Long Enzyme Mix.

Table 2.6 describes the typical PCR conditions used with Fermentas Long Enzyme Mix (Thermo Fisher Scientific Inc). The number of Denaturation-Annealing-Extension cycles was altered according to the concentration of DNA template used in the reaction and was often altered when optimising the reaction. The length of the extension step was varied according to the predicted size of the product being

amplified, allowing 1 minute of extension per Kilobase of product. The annealing temperature was also varied according to the melting temperatures of the oligonucleotide primers being used. This typically varied between 50°C and 60°C and was calculated based on the melting temperatures of the primers detailed in Appendix A.

Step	**Temperature**	**Time**	**# Cycles**
Initial Denaturation	**98°C**	**3 min**	**x1**
Denaturation	**96°C**	**20 sec**	**x10**
Annealing	**50°C - 60°C**	**30 sec**	
Extension	**68°C**	**60 sec/kb**	
Denaturation	**94°C**	**20 sec**	**x25**
Annealing	**50°C – 60°C**	**30 sec**	
Extension	**68°C**	**60 sec/kb**	
Final Extension	**72°C**	**10 min**	**x1**
Infinite Hold	**4°C**	∞	**x1**

Table 2.6: Standard conditions used for PCR with Fermentas Long PCR Enzyme Mix

Following PCR, products were either processed immediately or stored at 4°C until ready for use. For long-term storage, products were frozen at -20°C.

2.2.2.iv Rapid Amplification of 3’ cDNA Ends (3’ RACE) PCR

Amplification of 3’ ends of specific cDNA transcripts was performed using the Go-Taq Flexi DNA Polymerase Kit (Promega) with a gene specific forward primer and

an Oligo $V(dT)_{18}$ reverse primer. The Oligo $V(dT)_{18}$ primer consisted of 18 Ts, designed to anneal to the polyA tail of the mRNA transcripts, preceded by either A, C or G in a 1:1:1 ratio. As such, 3x standard volume of the reverse primer was necessary as only one third of primers would anneal correctly. The volumes of reagents used in 3' RACE PCR reactions are shown in Table 2.7. 3' RACE PCR reactions were typically performed in a total volume or 25 µl, or 50 µl when the products were to be isolated. Template RNA was typically added at an initial concentration of 20-100 ng/µl. All sets of PCR reactions contained a negative (template-free) control reaction to highlight any contamination of PCR reagents.

PCR Reagent	**Volume in 25 µl Reaction**	**Volume in 50 µl Reaction**
5X GoTaq Flexi Buffer	**5 µl**	**10 µl**
$MgCl_2$ Solution (25 mM)	**2 µl**	**4 µl**
dNTP Mix (10 mM each)	**0.5 µl**	**1 µl**
Forward Primer (10 pmol/µl)	**1 µl**	**2 µl**
Oligo $V(dT)_{18}$ Primer (10 pmol/µl)	**3 µl**	**6 µl**
Template DNA	**1 µl**	**2 µl**
GoTaq DNA Polymerase (5 u/µl)	**0.1 µl**	**0.2 µl**
H_2O	**12.4 µl**	**24.8 µl**
Total Volume	**25 µl**	**50 µl**

Table 2.7: Standard volumes of PCR reagents used in 3' RACE using GoTAQ DNA Polymerase

PCR was performed under the same conditions as standard PCR using GoTaq DNA Polymerase, with the annealing temperature calculated according to the melting temperature of the gene specific forward primer. Following PCR, products were either processed immediately or stored at 4°C until ready for use. For long-term storage, products were frozen at -20°C.

2.2.2.v. Purification of PCR Products

When visualisation of PCR products by Agarose Gel Electrophoresis (2.2.3.i) revealed that only one product had been produced, products were purified directly from solution using the QIAquick PCR Purification Kit (Qiagen). Unless stated otherwise, all centrifugation steps took place at 17,900 x *g* at room temperature.

The PCR reaction solution was added to a 1.5 ml microcentrifuge tube and 5 volumes of Buffer PB (containing Guanidine Hydrochloride and Isopropanol) were added to the tube to denature the PCR reagents and precipitate the DNA. The mixture was transferred to a QIAquick column and the column was placed into a 2 ml collection tube. If the volume of the mixture exceeded the maximum capacity of the column (800 µl), the mixture was divided into 800µl aliquots and the following step repeated until all of the mixture had been processed. The DNA was bound to the column by centrifugation for 1 minute. The flow through was discarded and the column place back into the same collection tube. The bound DNA was washed by adding 750 µl Buffer PE (containing Ethanol) and centrifuging for 1 minute. The flow through was discarded and the column was returned to the collection tube and subjected to a further minute of centrifugation to remove residual buffer. The QIAquick column was removed from the collection tube and placed in a clean 1.5 ml microcentrifuge tube. 50 µl Buffer EB ((containing 10 mM Tris.Cl pH8) was applied to the column filter and the PCR products were eluted by

centrifugation for 60 seconds. When a higher concentration of product was required, the volume of Buffer EB used was reduced to 30 µl and the column was allowed to stand for 1 minute prior to centrifugation. The concentration of eluted PCR products was measured using a Nanodrop Spectrophotometer (Thermo Fisher Scientific Inc.).

2.2.3 Gel Electrophoresis

2.2.3.i Agarose Gel Electrophoresis

PCR products were analysed using electrophoresis of agarose gels containing Ethidium bromide to confirm that the correct products of a predicted size had been produced. Typically, gels containing 1.5% agarose were used, however, agarose concentration was decreased to 1% when larger product sizes were predicted and increased to 2% when multiple bands were seen. Agarose gels were made by adding molecular grade agarose (Sigma-Aldrich) to 0.5x TBE Buffer in the correct w/v ratio to provide 1%, 1.5% or 2% gels. The mixture was heated with regular agitation to ensure that the agarose was completely dissolved. Ethidium bromide was added from stock (10 mg/ml) to a final concentration of 0.2 µg/ml. The gel was poured into a casting tray and a comb was placed with its teeth submerged in the gel, and was allowed to cool. Once cooled, the comb was removed and the gel was placed into a Mini-Sub Cell GT Cell (Bio-Rad) and covered in sufficient TBE buffer. For larger gels, either the Wide Mini-Sub Cell GT Cell or Sub-Cell GT Cell (Bio-Rad) was used according to size required. Samples were loaded directly into the wells left by the teeth of the gel casting combs. For clear samples, 6X Blue Loading Dye (New England Bioloabs) was added in a 1:5 ratio to provide blue colour for loading. For reference, 5 µl DNA marker ladder was loaded alongside samples to aid in band size determination. Different ladders were used depending on the predicted size of PCR

products. For products <1 kb in length, 100 bp DNA Ladder (New England Biolabs) was used. For products >1 kb in length, 1 Kb DNA Ladder (New England Biolabs) was used. Samples were run by applying 80 volts to the gel for 30 minutes using a PowerPac Basic Power Supply (Bio-Rad). When larger gels were run using a Sub-Cell GT Cell, the voltage was increased to 110 volts. Following gel electrophoresis, DNA was visualised by transillumination with UV light.

2.2.3.ii Extraction of PCR Products from Agarose Gel

PCR products were isolated from agarose gel using the QIAquick Gel Extraction Kit (Qiagen). This was used as an alternative to the QIAquick PCR Purification Kit (Qiagen) when PCR products showed multiple bands and only those of a specific size were to be extracted. Unless stated otherwise, all centrifugation steps took place at 17,900 x *g* at room temperature.

Using a clean scalpel, the desired band was excised from the agarose gel under UV light and placed into a clean 2 ml microcentrifuge tube and weighed. 3 volumes of yellow Buffer QG (containing Guanidine thiocyanate) were added to one volume of gel (for example, 100 mg ~ 100 µl) to aid in solubilisation. The tube was incubated at 50°C for 10 minutes, with regular agitation until the gel had completely dissolved. If the colour of the solution had changed from yellow to purple, 10 µl 3 m Sodium acetate (pH5) was added to lower the pH and restore the yellow colour. Once the gel was fully dissolved, 1 gel volume of room temperature isopropanol was added to the sample and mixed well. The mixture was then transferred to a QIAquick spin column and the column was placed into a 2 ml collection tube. If the volume of the mixture exceeded the maximum capacity of the column (800 µl), the mixture was divided into 800 µl aliquots and the following step repeated until all of the mixture

had been processed. To bind the DNA to the column, the sample was centrifuged for 1 minute. The flow through was discarded and the column returned to the same collection tube. 500 µl Buffer QG was added to the column and the sample was centrifuged for a further minute to remove any traces of agarose. The flowthrough was discarded and 750 µl Buffer PE (containing Ethanol) was applied to the filter. When the sample was to be directly used for sequencing, or other salt sensitive applications, the column was allowed to stand for 5 minutes. The sample was washed by centrifugation for 1 minute and the flow through was discarded. The column was placed back into the collection tube and subjected to a further 1 minute of centrifugation to remove residual ethanol from the filter. The column was removed from the collection tube and placed in a 1.5 ml microcentrifuge tube. To elute the DNA, 50 µl Buffer EB (containing 10 mM Tris.Cl pH8) was applied to the filter and the sample was centrifuged for 1 minute at 20,913 x *g*. When a higher concentration of eluted DNA was desired, the volume of Buffer EB was reduced to 30 µl and the sample was allowed to stand for 4 minutes prior to centrifugation. The concentration of eluted PCR products was measured using a Nanodrop Spectrophotometer (Thermo Fisher Scientific Inc.).

2.2.4 Nucleic Acid Restriction

2.2.4.i Digestion of DNA using Restriction Enzymes

A variety of different restriction enzymes were used to cut DNA based on recognised sequences, either 4 bases or 6 bases in length. All enzymes used were provided by New England Biolabs. Table 2.8 shows the volumes of different components used in a typical restriction digest using the four base cutter HaeIII (New England Biolabs). 1 unit of enzyme is typically the amount required to digest 1 µg DNA in a 50 µl

reaction in 60 minutes. However, a 10x overdigestion was used in order to neutralise any variability introduced by differences in DNA templates. Four different buffers are available from New England Biolabs for use in digestion reactions. Information provided with each enzyme indicated to the level of activity achieved by the enzyme in each of the available buffers. In all cases, the Buffer which allowed for the highest level of activity was used.

Component	**Volume**
HaeIII Restriction Enzyme (10 u/µl)	**1 µl**
DNA	**1 µg**
10X NE Buffer 2	**5 µl**
H_2O	**To 50 µl**

Table 2.8: Volumes of components used in a typical restriction digest.

Reactions were typically incubated at 37°C for 60 minutes to allow digestion to take place. The temperature and duration of incubation was varied according to the requirements of individual enzymes. Reactions were typically stopped using heat inactivation. This was performed by incubating the reaction mixture to 80°C for 20 minutes. The temperature and duration of heat inactivation used was varied according to the requirements of individual enzymes. Following digestion, restricted DNA could be purified using the Qiagen QIAquick PCR Purification Kit (2.2.2.v).

2.2.5 DNA Cloning

2.2.5.i DNA Ligation

DNA ligation was performed using T4 DNA Ligase with the pGEM-T Easy Vector System (Promega). Alongside DNA samples, ligation reactions were also performed using control insert DNA (positive control) and with no DNA insert (background control. 5 µl 2x Rapid Ligation Buffer was added to a clean 1.5 ml microcentrifuge tube with 1 µl pGEM-T Easy Vector. DNA inserts to be ligated were added in a 3:1 ratio of insert to the vector, equating to ~20 ng insert. For the positive control, 2 µl control insert DNA was added. 1 µl (3 units) of T4 DNA ligase were also added before H_2O was added to bring the reaction to a total volume of 10 µl. The reactions were mixed gently by pipetting and incubated at 4 °C overnight (minimum 16 hours).

2.2.5.ii Transformation of Competent Cells

Ligated DNA Vectors were transformed into Stratagene XL1-Blue Competent Cells (Agilent technologies). During transformation, an extra positive control was performed using the pUC18 control vector.

XL1-Blue competent cells (stored at -80 °C) were thawed on ice. Once thawed 100 µl of cells were pipetted into a 14 ml Falcon Polypropylene tube that had been pre-chilled on ice. 1.7 µl β-mercaptoethanol was added to each aliquot of cells. The tubes were swirled gently then incubate on ice for 10 minutes, with additional swirling every 2 minutes. Between 0.1 ng and 0.5 ng ligated sample DNA was added to the cells, with 1 µl pUC18 control DNA added to the positive control tube, and incubated for a further 30 minutes on ice. The cells were heat shocked at 42 °C in a water bath for precisely 45 seconds and incubated on ice for a further 2 minutes.

0.9 ml SOC medium, preheated to 42 °C, was added and the cells were incubated for 1 hour at 37 °C, shaking at 250 rpm.

LB agar plates were prepared containing Ampicillin at a final concentration of 50 μg/ml. To allow blue/white selection of colonies, X-gal (20 mg/ml) and IPTG (20%) were added at final concentrations of 800 ng/ml and 20 ng/ml respectively. 200 μl transformation mixture was applied to an LB agar plate and streaked evenly across the surface. For pUC18 control plates, 5 μl pUC18 transformation mixture was plated. Plates were incubated at 37 °C overnight (minimum 17 hours) to allow colony growth and colour development. Colonies that contained the desired insert developed a white colour whilst those that didn't developed a blue colour. Incubation for a further 2 hours at 4 °C helped to enhance colour development.

A number of white colonies were identified and transferred to a fresh plate using a heat sealed pipette tip. The presence of the desired insert within these colonies was further confirmed by colony PCR, using bacterial colonies as a source of template DNA by dipping the pipette tip into the PCR reaction mixture. PCR was then performed according to the same protocol as Standard PCR (2.2.2.ii) with SP6 and T7 primers (described in Appendix A), designed to amplify DNA inserts from the pGEM-T vector. Transferred colonies were incubated overnight (minimum 17 hours) at 37°C to allow further growth.

2.2.5.iii Preparation of Plasmids for Sequencing

Before plasmids were purified from colonies for sequencing, the colonies were grown in liquid culture. 2 ml of liquid LB media was added to a 14 ml Falcon Polyproylene tube with 2 μl Ampicillin (1000x dilution). The media was inoculated

with colonies know to contain the desired insert and incubated overnight (minimum 16 hours) at 37 °C, shaking at 250 rpm.

Plasmids were prepared for sequencing using the PureYield Plasmid Miniprep System (Promega). Unless stated otherwise, all centrifugation steps were performed at 17,900 x *g* at room temperature.

Following overnight incubation, liquid cultures were centrifuged at 3250 x *g* for 10 minutes to pellet the cells. The supernatant was discarded and the cells were resuspended in 600 µl LB media and transferred to a 1.5ml microcentrifuge tube. 100 µl Cell Lysis Buffer was added to the cells and mixed by inversion. Lysis was allowed to occur for no more than 2 minutes before 350 µl cold Neutralisation Solution (stored at 4 °C) was added and mixed thoroughly by inversion. Following complete neutralisation, indicated by the formation of a yellow precipitate, the mixture was centrifuged for 3 minutes to remove cellular debris. The supernatant was transferred to a PureYield Minicolumn and the column was placed in a PureYield Collection tube. The mixture was centrifuged for 15 seconds, the flow through was discarded and the column was returned to the same collection tube. 200 µl Endotoxin Removal Wash was added and the column was centrifuged for a further 15 seconds. Following centrifugation, 400 µl of Column Wash Solution was added to the column and the mixture was centrifuged for 30 seconds. The column was transferred to a clean 1.5 ml microcentrifuge tube and 30 µl Elution Buffer (10 mM Tris-HCl, 0.1 mM EDTA pH8.5) was applied directly to the column filter. The column was allowed to stand for 1 minute and then centrifuged for 15 seconds to elute the plasmid DNA. DNA was then processed immediately or stored at -20 °C. The concentration of eluted Plasmid DNA was measured using a Nanodrop Spectrophotometer (Thermo Fisher Scientific Inc.).

2.2.6 DNA Sequencing

2.2.6.i Direct DNA Sequencing

All direct sequencing of DNA was performed by external bodies. Samples sequenced by the Durham DNA Sequencing and Fragment Analysis Facility were sequenced using the Applied Biosystems 3730 DNA Analyser. Samples sequenced by Eurofins MWG Operon were sequenced using Applied Biosystems 3730XL DNA Analyser.

2.2.6.ii Next Generation DNA Sequencing.

a) 454 Sequencing

The 454 sequencing platform relies on the pyrosequencing reaction, detecting light emitted as nucleotides are incorporated into a complementary strand of DNA (Mardis, 2008). All 454 sequencing was performed by the Centre for Genomic Research, University of Liverpool using the Roche 454 GS FLX. Pyrosequencer.

b) Illumina Sequencing

The Illumina sequencing method relies on synthesis of a DNA strand using fluorescent labelled nucleotides which imaged following the incorporation of each base (Mardis, 2008). All Illumina Sequencing was performed by The Genome Analysis Centre, Norwich using the Illumina HiSeq2500 and Illumina MiSeq platforms.

2.2.7 Sequence Analysis of DNA

2.2.7.i Confirmation of Sequencing Results

DNA sequence data was produced in FASTA format and accompanied with chromatogram files to aid in the manual confirmation of the nucleotide sequence. Chromatograms were viewed using Chromas Lite (technelysium.co.au/?page_id=13), a free chromatogram viewer produced by Technelysium. DNA sequence was presented above the sequencing chromatogram and unclear bases were identified. The chromatogram peaks were used to manually 'call' ambiguous bases and to identify erroneous bases for removal. Following alterations, the FASTA sequence was altered accordingly.

2.2.7.ii Assembly of Sequence Contigs

Sequence contigs were combined by identifying areas of identical sequence at the ends of each of the smaller contigs when presented in FASTA format. DNA FASTA sequences were analysed using the NCBI Basic Local Alignment Search Tool BLASTN search (blast.ncbi.nlm.nig.gov/Blast.cgi) to align multiple contigs and identify regions of similar sequence. If homologous sequences were identified, they were used to combine the shorter sequence into a single, larger contig by removal of the sequence from one strand before joining the two sequences together. When possible, identical sequence was removed from the smaller of the two sequences to maintain continuity. Similarly, if one sequence was already anchored, having been previously joined to another, this sequence was preferred. The reverse complements of the sequences were used where necessary to maintain continuity. Reverse complementation of sequences was performed using The Sequence Manipulation Suite (www.bioinformatics.org/sms2).

In instances where genetic material had been obtained from cultivars of *Primula vulgaris*, the TGAC browser was used to convert the sequence from the cultivar into the wild type sequence. This served to remove and cultivar specific polymorphisms.

2.2.7.iii Alignment of DNA Sequences

DNA sequences were aligned using the EMBL-EBI ClustalW2 tool (www.ebi.ac.uk/tools/msa/clustalw2). Nucleotide sequences were entered in FASTA format and aligned based on their nucleotide sequence. The tool provided output by presenting the sequences above each other, displaying identical bases and highlighting regions unique to one sequence. The same tool was used for the alignment of amino acid sequences.

2.2.8 Annotation of DNA Sequences

2.2.8.i Translation of DNA Sequences

All nucleotide sequences were translated into Amino Acid sequences using the ExPASy Translate tool (www.expasy.org/tools). Nucleotide sequences were translated into six open reading frames; 3 forward and 3 reverse. The tool was also used to align translated sequence with its original nucleotide sequence.

2.2.8.ii Identification of Homologous Genes.

Nucleotide sequences were analysed using the NCBI BLAST to identify genes. Genes were identified based on homology with previously identified genes from other species using both the BLASTN tool, searching a nucleotide database using a nucleotide query, and the TBLASTX tool, searching a translated nucleotide database

using a translated nucleotide query. Only genes identified as homologous to genes from other plant species were recorded.

2.2.8.iii Genetic Annotation of Sequences

Following the initial identification of a gene containing nucleotide sequence, the sequence was translated and aligned to the known amino acid sequence of the homologous gene, obtained through the NCBI database, in order to identify any introns within the original nucleotide sequence. All open reading frames (ORFs) of the translated nucleotide sequence were aligned to the database sequence. Amino acids sequences were displayed alongside the original nucleotide sequences and intron-exon boundaries were identified in accordance with the GT-AG rule (Breathnach and Chambon, 1981). Start and stop codons were also identified and ORFs were combined to construct the amino acid sequence of the gene in conjunction with the original nucleotide sequence.

2.2.8.iv Syntenic Mapping of Genes

Following annotations of all genes found within nucleotide sequences, the amino acid sequences of each gene were used as queries in BLASTP searches, using protein queries to search protein databases, against a number of species-specific databases. The TAIR BLAST (www.arabidopsis.org/blast) tool was used to identify homologous genes from *Arabidopsis thaliana* whilst the Phytozome BLAST tool (www.phytozome.net) was used for other species. Upon identification of homologous genes, the locus of each gene was recorded and compared to the loci identified within *Primula* in order to identify any conservation of gene order.

CHAPTER THREE

Identification of the allelic origins of *Primula vulgaris* cv. Blue Jeans BACs

3.1 Introduction

3.1.1 Construction of the *P. vulgaris* cv. Blue Jeans BAC library

The construction of a BAC library, containing genomic DNA from Thrum *Primula vulgaris* cv. Blue Jeans individuals, provides an important source of sequence data from the area immediately surrounding the *Primula S* locus. Although not all of the BACs within the library have been characterised, many of the 54 BACs already identified are estimated to cover regions over 60Kb long with some examples, such as the BAC 32O2, up to 110Kb in length. Additionally, many BACs have also been shown to overlap with others within the library, suggesting that the two BAC sequences could be combined into a single, even larger sequence.

The *P. vulgaris* cv. Blue Jeans BACs have also been a valuable tool in the positioning of the three markers *SLL1*, *PvSLP1* and *Hose in Hose* relative to the *S* locus (Manfield *et al.*, 2005; Li *et al.*, 2007, 2008, 2011). By identifying *SLL1* within the BAC 32O2, *PvSLP1* within 81B15, and *PvGLO* (the locus responsible for the *Hose in Hose* mutation) within BAC 28O8, these three BACs could be used as starting points to identify other BACs surrounding them, using sequences from the end of each BAC to probe the BAC library and identify overlapping sequences. Using this method, a BAC walk has now been completed to identify 23 BACs from the region between the *S* locus and *PvGLO*, and the BACS identified by this method are shown in Figure 3.1 (Li *et al*., 2011).

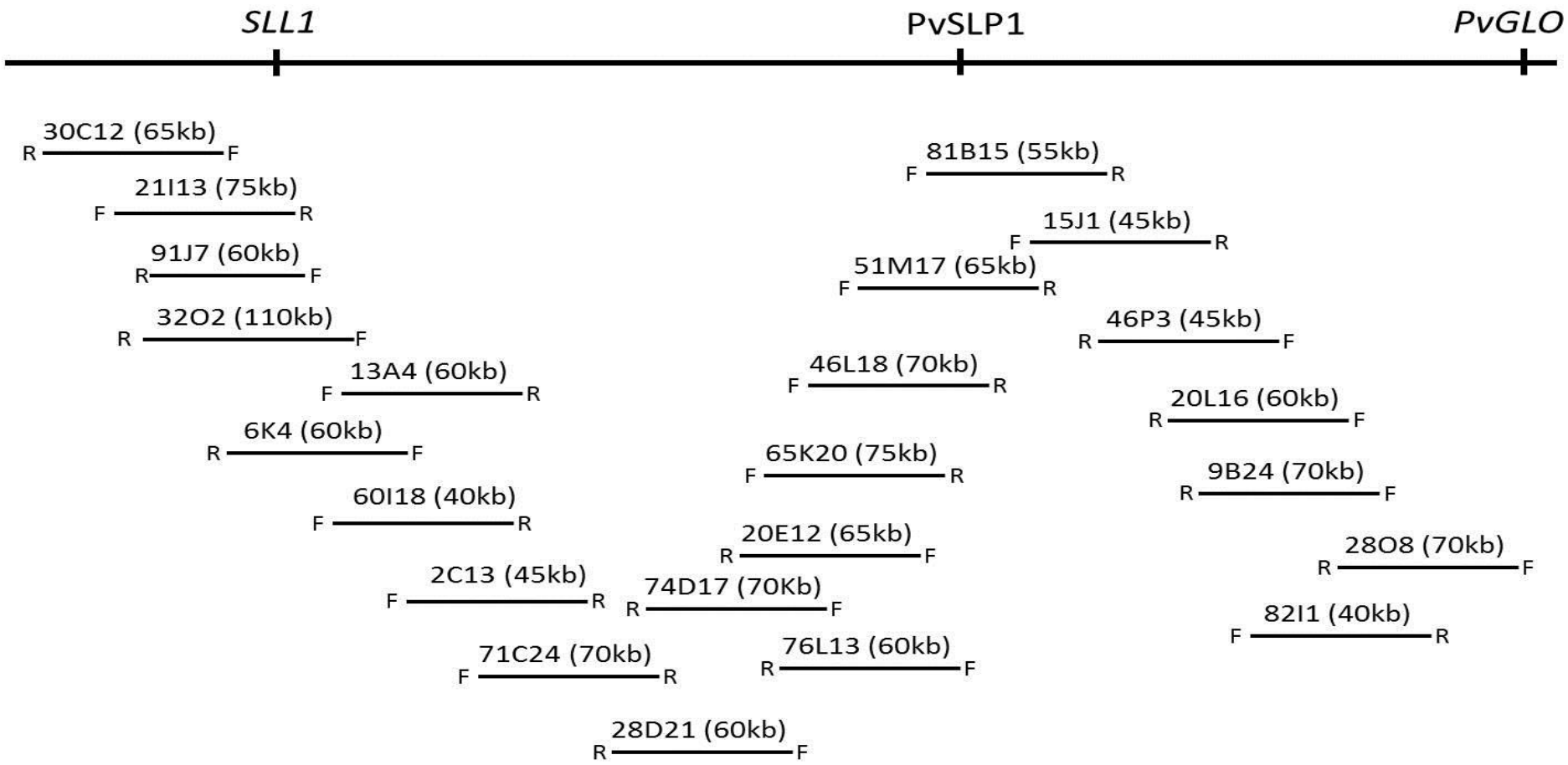

Figure 3.1: Relative positions of 23 BACs identified within the *P. vulgaris* cv. Blue Jeans BAC library. The F and R ends of each BAC are labelled. The positions of the *S* locus markers *SLL1*, *PvSLP1* and *PvGLO* and estimated sizes of BACs are shown. BACs are not shown to scale (Li *et al*., 2011).

Due to the large size of many of the BACs within the library, Direct DNA sequencing methods are unable to provide sequence data far beyond the ends of each BAC. Upon identification of each BAC and the sequencing of each end, the end thought to be the 5' end of the BAC was labelled as the F (Forward) end and the 3' end was labelled the R (Reverse) end, named in accordance with their direction relative to the *S* locus. However, on a number of occasions, subsequent probing of the BAC library using these F end and R end sequences revealed that the BAC was in the opposite orientation. An example of this is the BAC 46P3, in which the end sequences 46P3.R is found at the 5' end of the BAC and 46P3.F at the 5' end.

3.1.2. Attribution of BAC end sequences to *S* locus alleles

The region shown in Figure 3.1 is of particular significance given the nature of the three markers shown in the figure. *PvSLP1* is a Thrum specific polymorphism (Manfield *et al.*, 2005) and, in over 170 tests, no examples of recombination between *PvSLL1* and the *S* locus have been observed (Li *et al.*, 2007). However, *PvGLO* has been shown to recombine with the *S* locus (Li *et al.*, 2008). This suggests that the mechanisms which restrict recombination within the *S* locus, also preventing recombination between the locus and *PvSLL1* and *PvSLP1*, must not extend as far as *PvGLO*, breaking down within this region.

In order to characterise the region covered by the BACs shown in Figure 3.1, it is important to know which allele of the *S* locus each BAC was originally cloned from. Although all BACs were cloned from Thrum DNA, the heterozygous nature of Thrum individuals at the *S* locus means that the Pin allele for the locus was also

present within this original template DNA. As a result, the BAC library will contain a 50:50 mix of Pin and Thrum DNA.

Whilst these sequences could be combined to provide a consensus sequence for this region, particularly in the area near *PvGLO* where the Pin and Thrum alleles become less clearly defined, this may lead to the generation of incorrect data closer to the locus. Similarly, if, following the assembly of a sequence for this region, any further genes can be identified, it will be important to know if they are specific to either allele. This would be difficult if the allelic origins of the sequences are not known. Therefore, if it can be determined whether each BAC was originally cloned from the Pin or Thrum allele, those BACs cloned from the same allele could be sequenced and assembled to provide a reference sequence for a single allele of the *S* locus.

3.1.3. Selection of BACs for analysis

As discussed above, the mechanism which inhibits recombination within the *S* locus appears to break down within the region between *PvSLP1* and *PvGLO*. Consequently, particular attention will be paid to 4 BACs from this region: 81B15, 46P3, 9B24 and 28O8. Identified from Figure 3.1, these four BACs overlap sufficiently to form a link between the two markers whilst containing the least amount of redundant sequence due to overlaps. As such, if it can be demonstrated that these BACs have all been derived from the same allele of the *S* locus, they can be considered suitable candidates for sequencing and assembly of a single contiguous sequence linking the two markers.

However, in addition to these four BACs, a preliminary screen of other BACs, between *PvSLL1*and *PvSLP1* will also take place. For this purpose, 7 more BACs were selected from Figure 3.1 that could link the BACs 32O2 and 81B15: 6K4,

60I18, 71C24, 28D21, 65K20 and 51M17. Although these BACs are situated within the region thought to be protected from recombination, analysis of these sequences will provide a further insight into the allelic variety within the BAC library.

3.2 Results

3.2.1 *In vitro* analysis of BAC end sequences

Analysis of BAC end sequences was first approached using *in vitro* techniques to analyse the same BAC end sequences from a selection of Pin and Thrum individuals. All DNA samples used were extracted from individuals belonging to the Blue Jeans cultivar of *Primula vulgaris*.

3.2.1.i PCR amplification of BAC end sequences

Genomic DNA was extracted from 4 Pin and 4 Thrum individuals. BAC DNA was also extracted from BAC colonies stored at -80°C. Details of PCR primers and annealing temperatures used in PCR reactions can be seen in Appendix A.

Primers designed from BAC end sequences were used to amplify the BAC end sequence from 4 Pin and 4 Thrum genomic templates as well as a BAC DNA template. Figure 3.2 shows the results of PCR reactions amplifying the 5' end of the BACs 6K4, 60I18, 71C24, 65K20 and 51M17 as well as the amplification of the 3' end of BAC 28D21, as no sequence was available for the 5' end of this BAC. Figure 3.2 also shows that no amplification occurred when primers designed BAC end 71C24.F were used with 3rd Pin genomic DNA template. In addition to this, amplification of this BAC ends produced multiple bands from each template.

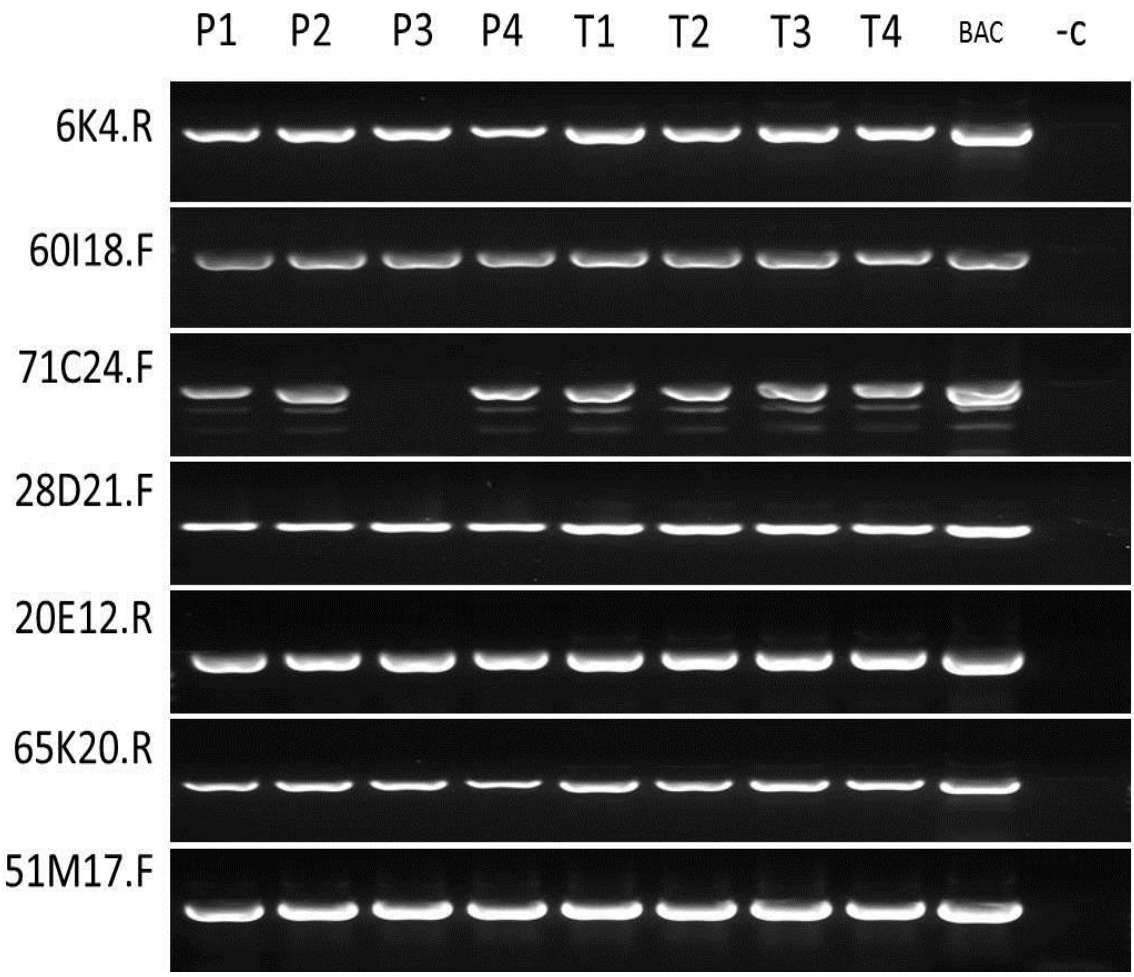

Figure 3.2: PCR amplification of BAC end sequences. BAC end sequences 6K4.R, 60I18.F, 71C24.F, 28D21.F, 20E12.R, 65K20.R and 51M17.F were amplified from 4 Pin and 4 Thrum genomic DNA templates and a BAC DNA template.

PCR was also used to amplify both BAC end sequences of the BACs 81B15, 46P3, 9B24 and 28O8 from the same Pin, Thrum and BAC templates. The results of these reactions can be seen in Figure 3.3. As shown in this figure, products were obtained from all BAC ends. However, primers from the F end of the BAC 46P3 were unable to amplify any products from the Thrum genomic DNA templates or from the third Pin genomic DNA template. For all other BAC ends however, no visible difference could be seen in the size of the products obtained.

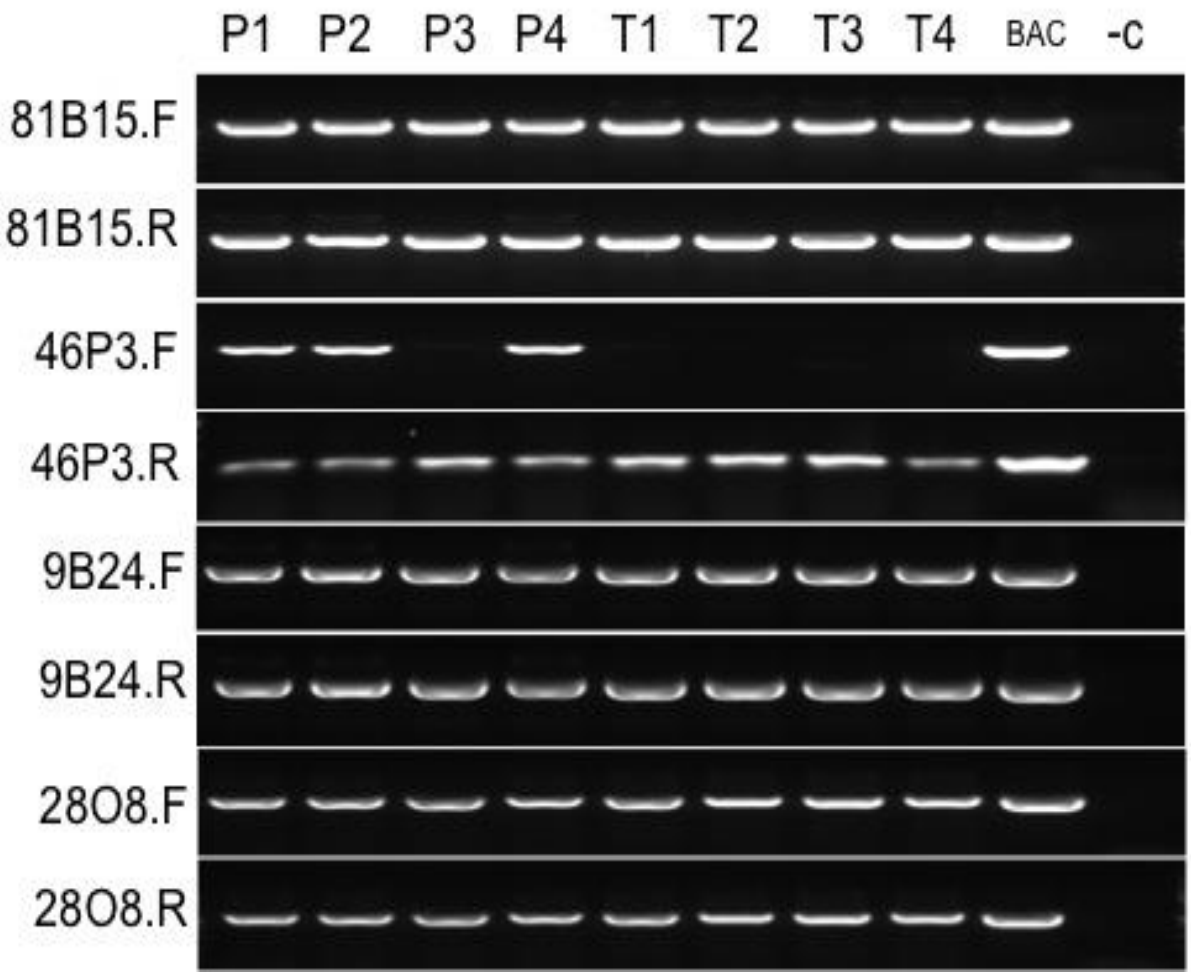

Figure 3.3: PCR amplification of both BAC ends from the BACs 81B15, 46P3, 9B24 and 28O8. Sequences were amplified from 4 Pin and 4 Thrum genomic DNA templates and a BAC DNA template.

3.2.1.ii Sequencing of amplified BAC end sequences

Following the amplification of the ends of the BACs 81B15, 46P3 (R end only), 9B24 and 28O8 by PCR, the amplified end genomic DNA sequences were analysed to identify polymorphisms. This process is described below for the BAC end 81B15.F and the same process was used for all 8 sequences.

The PCR reaction to amplify the BAC end sequence 81B15.F, shown above in 3.2.1.i, was repeated using 2 Pin and 2 Thrum genomic DNA templates. Following

gel electrophoresis, the products of the reactions were extracted and sequenced using the forward primer 81B15.FF by the Durham DNA Sequencing and Fragment Analysis Facility at Durham University. Upon receipt of the sequence data, the sequences were aligned using the EMBL-EBI ClustalW2 tool. Figure 3.4 shows the results of this alignment.

As seen in Figure 3.4, the majority of bases in the amplified sequences were the same in all 5 templates, with no difference between the Pin and Thrum sequences. However, it can also be seen that 7 SNPs exist between the two genomic templates, highlight in bold, including 5 substitutions, 1 insertion and 1 deletion. Figure 3.4 also shows that the same polymorphisms exist between the amplified BAC template and the Pin genomic DNA template. In addition to this, the NCBI blast2n tool was used to analyse the match between the two genomic templates and the BAC end sequence as a result of these SNPs.

```
T1                                                                ATGAATTTC**A**GG
T2                                                                ATGAATTTC**A**GG
BAC                                                               ATGAATTTC**A**GG
P1                                                                ATGAATTTC-GG
P2                                                                ATGAATTTC-GG
                                                                  ********* **

T1      ATTTGAAGATGCTTAATGTAGTTGATGAGCTTTCAGTTAAAGGTTATTTTTACGACTTTA
T2      ATTTGAAGATGCTTAATGTAGTTGATGAGCTTTCAGTTAAAGGTTATTTTTACGACTTTA
BAC     ATTTGAAGATGCTTAATGTAGTTGATGAGCTTTCAGTTAAAGGTTATTTTTACGACTTTA
P1      ATTTGAAGATGCTTAATGTAGTTGATGAGCTTTCAGTTAAAGGTTATTTTTACGACTTTA
P2      ATTTGAAGATGCTTAATGTAGTTGATGAGCTTTCAGTTAAAGGTTATTTTTACGACTTTA
        ************************************************************


T1      ATATTTGCATGTATGATGTATGTT-AGTGAAGAACGGTGATGAACTTTGTTTTGGAATTG
T2      ATATTTGCATGTATGATGTATGTT-AGTGAAGAACGGTGATGAACTTTGTTTTGGAATTG
BAC     ATATTTGCATGTATGATGTATGTT-AGTGAAGAACGGTGATGAACTTTGTTTTGGAATTG
P1      ATATTTGCATGTATGATGTATGTT**C**AGTGAAGAACGGTGATGAACTTTGTTTTGGAATTG
P2      ATATTTGCATGTATGATGTATGTT**C**AGTGAAGAACGGTGATGAACTTTGTTTTGGAATTG
        ************************ ***********************************


T1      GGATTTACTTATTATGCAGATTCTGCTGTTAC**A**ATTTGGTCTGATTTGACGATTTTATGC
T2      GGATTTACTTATTATGCAGATTCTGCTGTTAC**A**ATTTGGTCTGATTTGACGATTTTATGC
BAC     GGATTTACTTATTATGCAGATTCTGCTGTTAC**A**ATTTGGTCTGATTTGACGATTTTATGC
P1      GGATTTACTTATTATGCAGATTCTGCTGTTAC**T**ATTTGGTCTGATTTGACGATTTTATGC
P2      GGATTTACTTATTATGCAGATTCTGCTGTTAC**T**ATTTGGTCTGATTTGACGATTTTATGC
        ******************************** *************************
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```
T1      CTAGTGTCATGTTGCTTAGTCATTTGTGTTCACTAAGTTTCAGAATCTGACAATAATACA
T2      CTAGTGTCATGTTGCTTAGTCATTTGTGTTCACTAAGTTTCAGAATCTGACAATAATACA
BAC     CTAGTGTCATGTTGCTTAGTCATTTGTGTTCACTAAGTTTCAGAATCTGACAATAATACA
P1      CTAGTGTCATGTTGCTTAGTCATTTGTGTTCACTAAGTTTCAGAATCTGACAATAATGCA
P2      CTAGTGTCATGTTGCTTAGTCATTTGTGTTCACTAAGTTTCAGAATCTGACAATAATGCA
        ************************************************************ **

T1      GGATACTTTAGCAGTGTTACAACCATGCTATTAATCTTTACCATAATAATGGTTTTTAAC
T2      GGATACTTTAGCAGTGTTACAACCATGCTATTAATCTTTACCATAATAATGGTTTTTAAC
BAC     GGATACTTTAGCAGTGTTACAACCATGCTATTAATCTTTACCATAATAATGGTTTTTAAC
P1      GGATACTTTAGCAGTGTTACAGCCATGCTATTAATCTTTACCATAATAATGGTTTTTAAC
P2      GGATACTTTAGCAGTGTTACAGCCATGCTATTAATCTTTACCATAATAATGGTTTTTAAC
        ********************* ************************************

T1      CAAATTTTCTCCCTATAGCGTGTATAAAAACAAAGAATAATAAGAAAAGGAAAAAAAATC
T2      CAAATTTTCTCCCTATAGCGTGTATAAAAACAAAGAATAATAAGAAAAGGAAAAAAAATC
BAC     CAAATTTTCTCCCTATAGCGTGTATAAAAACAAAGAATAATAAGAAAAGGAAAAAAAATC
P1      CAAATTTTCTCCCTATAGCGTGTATAAAAACAAAGAATAATAAGAAAAGGAAAAAAATTC
P2      CAAATTTTCTCCCTATAGCGTGTATAAAAACAAAGAATAATAAGAAAAGGAAAAAAATTC
        ************************************************************ **

T1      CGGGTCAAACGGGTCGGGTATAAACGGGTCGTGTCGGGTTACGTGCGGCTTGATGCCCGG
T2      CGGGTCAAACGGGTCGGGTATAAACGGGTCGTGTCGGGTTACGTGCGGCTTGATGCCCGG
BAC     CGGGTCAAACGGGTCGGGTATAAACGGGTCGTGTCGGGTTACGTGCGGCTTGATGCCCGG
P1      CGGGTCAAACGGGTCGGGTATAAACGGGTCGTGTCGGGTTACGTGCGGCTTGATGCCCGG
P2      CGGGTCAAACGGGTCGGGTATAAACGGGTCGTGTCGGGTTACGTGCGGCTTGATGCCCGG
        ************************************************************


T1      GTCGGGTCGGATTTTGAGAAACCCGGCCCAATTGCCATCCCTAATTCTATTGCTTGCAAA
T2      GTCGGGTCGGATTTTGAGAAACCCGGCCCAATTGCCATCCCTAATTCTATTGCTTGCAAA
BAC     GTCGGGTCGGATTTTGAGAAACCCGGCCCAATTGCCATCCCTAATTCTATTGCTTGCAAA
P1      GTCGGGTCGGATTTTGAGAAACCCGGCCCAATTGCCATCCCTAATTCTATTGCTTGCAAA
P2      GTCGGGTCGGATTTTGAGAAACCCGGCCCAATTGCCATCCCTAATTCTATTGCTTGCAAA
        ************************************************************

T1      TTAACTCAAGCAAAGGCATCAAAATAATACCATAAACAGGATAACAACTATTAGTCTATT
T2      TTAACTCAAGCAAAGGCATCAAAATAATACCATAAACAGGATAACAACTATTAGTCTATT
BAC     TTAACTCAAGCAAAGGCATCAAAATAATACCATAAACAGGATAACAACTATTAGTCTATT
P1      TTAACTCAAGCAAAGGCATCAAAATAATACCATAAACAGGATAACAACTATTAGTCTATT
P2      TTAACTCAAGCAAAGGCATCAAAATAATACCATAAACAGGATAACAACTATTAGTCTATT
        ************************************************************

T1      ATACCATAGCAATGTACAAGCATTTTATTGTAACCACGGCTCAGA
T2      ATACCATAGCAATGTACAAGCATTTTATTGTAACCACGGCTCAGA
BAC     ATACCATAGCAATGTACAAGCATTTTATTGTAACCACGGCTCAGA
P1      ATACCATAGCAATGTACAAGCATTTTATTGTAACCACGGCTCAGA
P2      ATACCATAGCAATGTACAAGCATTTTATTGTAACCACGGCTCAGA
        *********************************************
```

Figure 3.4: Alignment of 81B15.F sequences. Sequences were amplified using BAC end 81B15.F primers and sequenced using the primer 81B15.FF. Low quality sequence data at both 5' and 3' ends has been removed. * indicates a match between all sequences for this base.

This 98.7% match rate between the Pin and BAC templates, compared to the 100% match seen between BAC and Thrum, suggests that the BAC sequence has been derived from the Thrum allele.

The same alignment process was performed for the end sequences of 46P3, 9B24 and 28O8 as well as 81B15.R. Table 3.1 shows the match rates seen between these sequences and the original BAC sequence and the proposed allelic identity of each BAC end based upon these percentages. As seen in Table #, this calculation suggested that BACS 81B15 and 9B24 were both derived from Thrum, whilst 46P3 was originally cloned from the Pin allele. However, Table 3.1 also suggests that the two ends of 28O8 have different identities, with the 28O8.F showing a closer match to the Thrum genomic DNA sequence whereas 28O8.R shows more homology to Pin.

BAC	**End**	**Sequence Length (bp)**	**No. non-matching bases**		**Suggested Identity**
			Pin	**Thrum**	
81B15	**F**	**647**	**8**	**0**	**Thrum**
	R	**638**	**27**	**5**	**Thrum**
46P3	**F**	**322**	**2**	**N/A**	**Pin**
	R	**217**	**10**	**25**	**Pin**
9B24	**F**	**649**	**597**	**181**	**Thrum**
	R	**625**	**22**	**10**	**Thrum**
28O8	**F**	**542**	**10**	**9**	**Thrum**
	R	**640**	**14**	**149**	**Pin**

Table 3.1: Homology between 81B15, 46P3, 9B24 and 28O8 end sequences and Pin and Thrum genomic DNA samples. Suggested allelic identities are included.

3.2.1.iii Restriction digestion of BAC end 81B15.F

Following sequencing of the BAC end 81B15.F, the sequence was analysed using the online Restriction of DNA Sequences tool (Bikandi *et al*., 2004) to identify possible restriction sites within 81B15.F caused by the 7 SNPs seen in Figure 3.4. Table 3.2 shows the restriction sites for the enzyme HpyCH4V identified by this tool, including the identified cleavage sites and the expected fragment sizes following digestion with the enzyme, including a restriction site at base 264 found only in the Pin sequence.

Individual	Full Sequence Length (bp)	Cleavage Sites	Expected Fragment Sizes (bp)
T1	**614**	**92/160/500**	**92/68/340/114**
T2	**615**	**93/161/501**	**93/68/340/114**
BAC	**644**	**127/195/535**	**137/68/340/109**
P1	**616**	**93/162/264/502**	**93/69/102/238/144**
P2	**613**	**90/159/261/499**	**90/69/102/238/144**

Table 3.2: HpyCH4V cleavage sites in 81B15.F. Predicted cleavage sites of sequences amplified from BAC end 81B15.F when digested with restriction enzyme HpyCH4V. The predicted diagnostic fragment, present in Thrum only, is highlighted in bold.

81B15.F was amplified from same genomic DNA templates as in 3.2.1.ii and the products were digested using HypCH4V. Figure 3.5 shows the result of gel electrophoresis of these products, in which a size difference can be seen between Pin and Thrum DNA. It can also be seen that the digestion of BAC DNA has produced the same banding pattern as Thrum (Li *et al*., 2011).

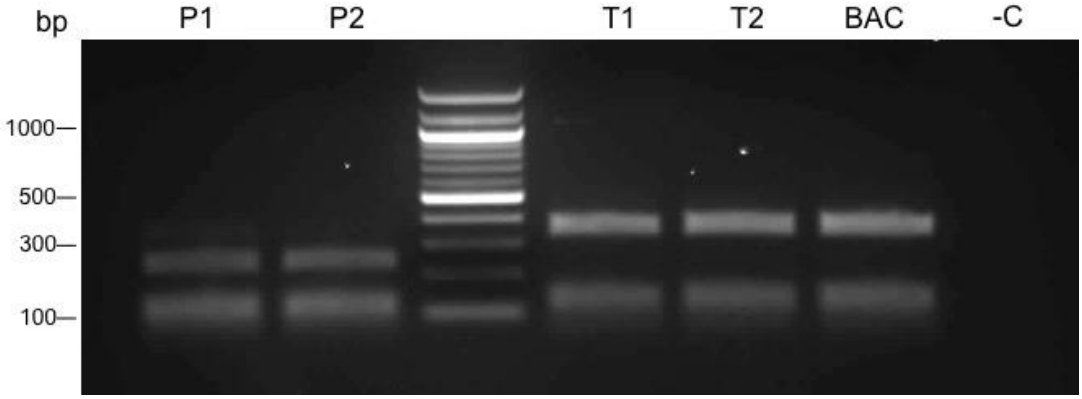


Figure 3.5: HpyCH4V digestion of 81B15.F. Gel electrophoresis image of 81B15.F amplified from Pin and Thrum genomic DNA and BAC DNA and digested using enzyme HpyCH4V.

3.2.2. Analysis of BAC end sequences using whole genome sequence data

The availability of whole genome sequence data provided a further resource of Pin and Thrum DNA data with which BAC end sequences could be compared. All available end sequences from BACs shown in Figure 3.1 were used as queries to BLAST search both the prim-allpin-k71-scaffolds and the prim-allthrum-k71-scaffolds databases in the TGAC *Primula* browser. For each BAC end sequence, the highest scoring match was recorded from each database. Comparison of the Pin and Thrum scores therefore suggested an allelic identity of the BAC end based on homology to genomic DNA data. Table 3.3 shows the results of each search, including the contig identified from each database and the suggested identity of each BAC end based on the match scores.

BAC	End	Sequence Length (bp)	Pin			Thrum			Suggested ID	
			Contig	No. non-matching bases	Score	Contig	No. non-matching bases	Score	End	BAC
30C12	F	601	4073181	5	1054	4749923	39	906	Pin	Pin
21O13	F	565	4228625	68	818	4859382	31	523	Thrum	Thrum
	R	532	4237983	6	922	2858176	6	922	P/T	
91J7	F	610	4237983	1	1095	4858176	0	1101	Thrum	Thrum
	R	605	4098143	8	1058	4811196	8	1058	P/T	
32O2	F	689	4147165	24	1124	4753997	24	1124	P/T	Pin
	R	615	4237983	55	854	4858176	56	848	Pin	
13A4	F	639	4207260	39	877	4858339	38	845	Thrum	P/T
	R	348	4198972	5	773	4865257	3	778	Pin	
6K4	F	639	4160005	13	1099	4809303	13	1099	P/T	Pin
	R	348	4197012	7	426	4838499	4	284	Pin	
60I18	F	455	4160005	7	780	4809303	4	792	Thrum	Thrum
	R	508	4229229	7	877	4864670	5	890	Thrum	
2C13	F	501	4038816	38	749	4851925	28	749	P/T	Thrum
	R	637	4036066	5	1133	4845017	3	1137	Thrum	
71C24	F	616	4036066	10	1058	4845017	8	1061	Thrum	Thrum
	R	644	4064944	42	792	4648977	43	946	Thrum	
28D21	F	439	4242654	62	259	4867444	62	259	P/T	P/T
74D17	F	516	4231369	19	809	4866419	20	805	Pin	P/T
	R	612	4240935	11	489	4839021	11	495	Thrum	
76L13	F	672	4241439	28	1083	4865433	7	932	Pin	Pin
	R	611	4149516	43	863	4858435	43	856	Pin	
20E12	F	656	4214458	29	1032	4829678	32	1023	Pin	Pin
	R	693	4235328	4	1232	4862708	4	1232	P/T	

65K20	**F**	**621**	**4235328**	**4**	**1099**	**4862708**	**4**	**1099**	**P/T**	**P/T**
	R	**627**	**4242639**	**1**	**1122**	**4829678**	**1**	**1122**	**P/T**	
46L18	**F**	**695**	**4214458**	**3**	**1238**	**4639676**	**4**	**1234**	**Pin**	**P/T**
	R	**681**	**4230966**	**42**	**646**	**4937461**	**49**	**657**	**Thrum**	
51M17	**F**	**700**	**4242639**	**2**	**1254**	**4829678**	**2**	**1254**	**P/T**	**Pin**
	R	**655**	**4243302**	**0**	**1182**	**4848079**	**1**	**1177**	**Pin**	
81B15	**F**	**647**	**4244749**	**6**	**1133**	**4854631**	**0**	**1162**	**Thrum**	**Thrum**
	R	**638**	**4243302**	**0**	**906**	**4845839**	**0**	**906**	**P/T**	
15J1	**F**	**678**	**4226544**	**20**	**1155**	**4821479**	**9**	**1159**	**Thrum**	**Thrum**
	R	**693**	**4245353**	**48**	**1032**	**4859308**	**47**	**1036**	**Thrum**	
46P3	**F**	**322**	**4226293**	**17**	**302**	**4865836**	**17**	**302**	**P/T**	**Pin**
	R	**217**	**4197906**	**17**	**311**	**4867325**	**18**	**307**	**Pin**	
20L16	**F**	**609**	**4243302**	**15**	**1056**	**4845839**	**16**	**1050**	**Pin**	**P/T**
	R	**698**	**4239635**	**4**	**1240**	**4827896**	**3**	**1243**	**Thrum**	
9B24	**F**	**649**	**4059405**	**9**	**1088**	**4801597**	**44**	**922**	**Pin**	**P/T**
	R	**625**	**4226544**	**5**	**1104**	**4821479**	**3**	**1113**	**Thrum**	
82I1	**F**	**590**	**4228148**	**2**	**967**	**4819391**	**8**	**1040**	**Thrum**	**Thrum**
	R	**520**	**4217967**	**13**	**834**	**4847260**	**13**	**834**	**P/T**	
28O8	**F**	**542**	**4231296**	**1**	**973**	**4844373**	**1**	**973**	**P/T**	**P/T**
	R	**640**	**4188597**	**3**	**1137**	**4849460**	**3**	**1137**	**P/T**	

Table 3.3: Homology of BAC end sequences to Pin and Thrum genomic DNA. The highest scoring results of BLAST searches against Pin and Thrum genomic DNA contigs using BAC end sequences are shown as well as predicted allelic identities.

All contigs can be found within the TGAC browser when the following prefixes are attached to the contig numbers shown in Table 3.3:

- All Pin contigs, from the prim-allpin-k71-scaffolds database, require the prefix pin_all_wgs_ab_71_
- All Thrum contigs, from the prim-allthrum-k71-scaffolds database, require the prefix thrum_all_wgs_ab_71_

Table 3.3 also shows a suggested allelic identity of each BAC, based on the matches identified for each BAC end, as either Pin, Thrum or P/T when no difference could be seen between the matching contigs identified from both Pin and Thrum databases. In instances where one BAC end suggested an identity of Pin or Thrum but its opposite end is mark P/T, the identity from the first BAC (called from Pin or Thrum) was assumed. As seen in Table 3.3, 7 BACs were given the suggested identity of Pin and 8 BACs were given the suggested identity of Thrum whilst 8 could not be decided.

3.3 Discussion

3.3.1 Allelic origins of BACs 81B15, 46P3, 9B24 and 28O8

The results presented in this chapter have made it possible to suggest whether BACs within the *P. vulgaris* cv. Blue Jeans BAC library were originally cloned from the Pin or thrum allele of the *S* locus. Whilst a suggested identity has been obtained for each of the BACs between the *S* locus and *PvGLO*, shown in Figure 3.1, the main focus has been on the four BACs 81B15, 46P3, 9B24 and 28O8 that collectively link the *PvSLP1* to *PvGLO*. As discussed in 3.1, this region has a particular significance

as it is the area between the outer boundary of the *S* locus and the nearest known *S* locus marker, and thought to contain the other known *S* locus linked gene *sepaloid*.

3.3.1.i Analysis using *in vitro* methods

The initial PCR amplification of both F and R end sequences from the four BACs, shown in Figure 3.3, revealed no significant size differences between sequences when they were amplified from Pin and Thrum genomic DNA templates. However, Figure 3.3 also shows that no product was obtained when the primers for BAC end 46P3.F were used with a Thrum genomic DNA template. In contrast to this, the same primers successfully amplified the end sequence from 3 of the 4 Pin genomic DNA samples and the DNA extracted from the 46P3 BAC colony. This result suggests that differences must exist when this sequence is found within the Pin and Thrum genomes. The most likely cause for this is a sequence polymorphism in the sequence used as a primer, resulting primers that cannot successfully anneal to the Thrum template. Alternatively, this could also be caused by a large insertion into the Thrum genome that increased the size of the amplicon beyond the capabilities of the *Taq* polymerase used. The reason that no product could be amplified from the third Pin genomic DNA template remains unknown and subsequent attempts to optimise the PCR reaction were also unsuccessful. However, the products seen for 3 of the Pin genomic DNA templates, in addition to the product seen when a BAC template was used, strongly suggests that the sequence at the F end of 46P3 was originally derived from the Pin allele of the *S* locus. Therefore, it can also be assumed that the entire BAC was derived from this allele, even though no differences can be seen in Figure 3.3 seen between the Pin and Thrum results when 46P3.R was amplified.

As described in 3.2.1.ii for the example of 81B15.F, two products amplified from Pin DNA and two products amplified from Thrum DNA were sequenced and aligned to the original BAC sequence. As seen in the example shown in Figure 3.4, this allowed for the identification of SNPs between the sequences amplified from each template. Further to this, comparison with the sequence derived from the relevant BAC colony was able to show if the BAC sequence contained the same polymorphisms. In the example of 81B15, shown in Figure 3.4, this demonstrated that the BAC sequence possessed the same base changes seen in the Thrum sequences. These data are summarised in Table 1.1, which showed that the 7 SNPs identified led to a 1.3% difference in the Pin and BAC sequences, and provided evidence that 81B15.F was derived from the Thrum allele.

This same approach, when applied to the other BAC end sequences suggested that 81B15 and 9B24 originated from the Thrum allele of the *S* locus and 46P3 from the Pin allele, whilst the 2 ends of 28O8 appeared to have been derived from different alleles.. Although the BAC end 28O8.R showed a considerably higher level of similarity to the sequence amplified from Pin genomic DNA, alignment of 28O8.F to genomic sequences appeared more similar to Thrum, suggesting that the allele from which 28O8 was originally cloned had recombined. Given the relatively large distance between this BAC and the *S* locus, it is possible that the mechanism preventing recombination has broken down in the region covered by this BAC. This is supported by the presence of *PvGLO*, a gene known to recombine, within this BAC.

With the exception of 46P3.F, for which no Thrum sequence was obtained, 9B24.F and 28O8.R, the differences in the % matches of the BAC sequences to the amplified Pin and Thrum genomic sequences were very small. For example, 28O8.F was called

as Thrum based on a 0.2% difference in the matches between the BAC sequence and genomic sequences. These extremely small differences are not unexpected as the majority of SNPs seen were substitutions, leading to two sequences that were largely identical. However, the nature of the polymorphisms, as a single change in base, means that it is important that the sequence obtained from PCR products is as accurate as possible, as sequencing errors or incorrect calling of a base could lead to the incorrect identification of a BAC end as Pin or Thrum.

In the example of 81B15.F, as described in 3.2.1.iii, the polymorphisms seen in sequencing could be confirmed by restriction digest. As shown in Table 3.2, a restriction site for the enzyme HpyCH4V was identified at base 264 of the Pin sequence that coincided with a SNP. As such, an extra restriction site existed in the Pin sequence that could not be seen in either Thrum or BAC sequences. As seen in Figure 3.5, digestion of the 81B15.F from Pin, Thrum and BAC templates with HpyCH4V produced bands of a smaller size in Pin, providing more evidence of 81B15 as a Thrum linked BAC (Li *et al*., 2011).

3.3.1.ii Analysis using *in silico* methods

Comparisons between known BAC end sequences and newly available whole genome data largely supported the data discussed in 3.3.1.i. The prim-allpin-k71-scaffolds and the prim-allthrum-k71-scaffolds databases within the TGAC *Primula* browser provided large repositories of sequence data obtained from a variety of Pin and Thrum individuals. Therefore, by using BAC end sequences to BLAST search these databases, it was possible to quickly search multiple Pin or Thrum genomes to isolate the contigs with the most similarity.

Table 3.3 shows the results of all of the searches performed against these databases and the results for 81B15, 46P3, 9B24 and 28O8 are repeated below in Table 3.4.

BAC	End	Sequence Length (bp)	Pin			Thrum			Suggested ID	
			Contig	No. non-matching bases	Score	Contig	No. non-matching bases	Score	End	BAC
81B15	F	647	4244749	6	1133	4854631	0	1162	Thrum	Thrum
	R	638	4243302	0	906	4845839	0	906	P/T	
46P3	F	322	4226293	17	302	4865836	17	302	P/T	Pin
	R	217	4197906	17	311	4867325	18	307	Pin	
9B24	F	649	4059405	9	1088	4801597	44	922	Pin	P/T
	R	625	4226544	5	1104	4821479	3	1113	Thrum	
28O8	F	542	4231296	1	973	4844373	1	973	P/T	P/T
	R	640	4188597	3	1137	4849460	3	1137	P/T	

Table 3.4: Repeated homology results for 81B15, 46P3, 9B24 and 28O8. Highest scoring results of BLAST searches against Pin and Thrum genomic DNA contigs for BACs 81B15, 46P3, 9B24 and 28O8.

As seen in Table 3.4, the same overall identities are suggested for BACs 81B15 and 46P3 as suggested using *in vitro* methods. However, this alternative method was unable to determine an identity for 9B24, with both ends showing a greater similarity to different alleles. This is in sharp contrast to the results previously discussed. When sequenced and aligned to the BAC sequence previously, 9B24.F showed a significantly higher level of similarity to the sequence amplified from Thrum than that amplified from Pin, a difference of 64.1%. Similarly, Table 3.4 shows that 46P3.F identified sequences in both Pin and Thrum databases that both showed the same level of similarity to the query sequence. Again, this is very different to the results of the first PCR screen, shown in Figure 3.3, in which no product could be amplified from Thrum genomic DNA. However, as discussed in 3.3.1.i, PCR may

have failed due to polymorphisms within the primer sequences in Pin and Thrum. Subsequently, when the full BAC sequence was used to search the genomic databases, a match could be obtained based on similarities beyond the primer regions.

In addition to these differences, Table 3.4 also shows that neither end of 28O8 showed a greater similarity to one allele, finding hits scoring the same in each database. This shows disparity to the results discussed in 3.3.1.i, which suggest 28O8.F was derived from the Pin allele and 28O8.R to be from Thrum.

A possible explanation for the differences in the suggested allelic identities is a result of the individuals from which the sequence data was obtained. As described in 3.1, the BACs referred to in this chapter were cloned from the *Blue Jeans* cultivar of *P. vulgaris*. As such, it is very likely that polymorphisms will exist between the *P.vulgaris* cv. Blue Jeans derived BAC sequences and the wild type Primrose genome sequences used in this comparison. As a result, it is possible that any differences in the % match seen for Pin and Thrum have been exaggerated by natural variation between cultivars instead of between Pin and Thrum.

Another explanation for the different allelic identities suggested by the two methods is a result of the heterozygous nature of all Thrum individuals. As described in 1.5.2, all Thrum individuals must possess both Pin and Thrum alleles, with the dominant Thrum allele responsible for the observed phenotype. Consequently, whole genome sequences obtained from Thrum individuals will also contain an amount of Pin genomic DNA. The result of this is that sequences such as 28O8.R, which had been characterised as Pin through *in vitro* methods, could identify a contig within the Thrum database with an equal score to the one found in the Pin database.

The combination of *in vitro* and *in silico* methods strongly suggests that 81B15 was originally cloned from the Thrum allele of the *S* locus and 46P3 from the Thrum. However, whilst *in vitro* methods suggested 9B24 as a Thrum-linked BAC, this could not be supported using *in silico* methods and neither method could suggest an allelic origin for 28O8. Additionally, even though an identity has been suggested for 81B15 and 46P3, discrepancies exist between the two methods and, with the exceptions of examples such as 81B15.F, it is difficult to be certain that the proposed allelic origins are true. As such, while these BACs could be reliably used to form a single sequence spanning the region adjacent to the *S* locus, the results presented in this chapter suggest that they contain a mix of Pin and Thrum DNA. Consequently, this makes them unsuitable for use in the identification of genes within this region, as it would not be possible to determine if these genes were Pin or Thrum specific. Similarly, if any allele specific genes were identified which bridge junction between BACs, genetic data might be lost with the transition from one allele to the other.

3.3.2 Allelic origins of remaining BACS

3.3.2.i Analysis using PCR amplification

The initial PCR amplification of the BAC ends 6K4.R, 60I18.F, 71C24.F, 28D21.F, 20E12.R, 65K20.R and 51M17.F, shown in Figure 3.2, showed no significant size differences between the products amplified from Pin, Thrum and BAC templates. However, Figure 3.2 also shows that no product was amplified when primers for 71C24.F were used with the third Pin genomic DNA template. The reason for this absence of product remains unknown and sequencing of successfully amplified amplicons showed no differences between Pin and Thrum sequences (data not shown). In addition to the absence of any product for P3, multiple bands can also be

seen in for 71C24.F in Figure 3.2. The most likely cause for these was a loss of specificity when the primers annealed to the original template DNA and optimisation of the PCR protocol used should remove these.

As discussed in 3.3.1.ii, the heterozygous nature of the Thrum genome limits the viability of PCR alone as a method of determining the allelic origins of BACs. When PCR is used with a Thrum genomic DNA template, it cannot be certain that only the Thrum allele will be amplified and it is possible that the Pin allele is amplified from both templates. Subsequently, any polymorphisms that exist within the BAC end sequences shown in Figure 3.2 may be masked by amplification of the Pin allele in place of Thrum. Similarly, as demonstrated in Figure 3.4, many of the polymorphisms seen between alleles were mostly SNPs. As such, gel electrophoresis would not adequately separate the products to observe size differences.

3.3.2.ii Analysis using *in silico* methods

Comparison of all of the end sequences from the BACs shown in Figure 3.1 has further illustrated the difficulty in determining the allelic origins of each BAC. As seen in Table 3.3, BLAST searches of all remaining BAC end sequences suggested that 6 BACs (30C12, 32O2, 6K4, 76L13, 20E12 and51M17) had been derived from the Pin allele of the *S* locus and 7 (21O13, 91J7, 60I18, 2C13, 71C24, 15J1 and 82I1) were derived from Thrum. However, a further 6 BACs (13A4, 28D21, 74D17, 65K20, 46L18 and 20L16) could not be assigned to either allele using this method.

The explanations of this inability to assign these six BACs to either allele are the same as those discussed in 3.3.1.ii. Variation between wild type *P. vulgaris* and the Blue Jeans cultivar may be responsible for base miss matches rather than a difference in allelic identity. Similarly, the presence of the Pin allele within the

Thrum genome means that the BLAST searches shown in Table 3.3 may be identifying Pin sequence from the Thrum database.

Although the focus of the chapter was to determine the allelic origins of the BACS 81B15, 46P3, 9B24 and 28O8, Figure 3.2 and Table 3.3 serve to demonstrate the similarities seen between BAC end sequences throughout the region between *PvSLL1* and *PvGLO*, and the subsequent difficulty in determining the origins of each BAC. Although one method of analysis may suggest that a BAC is derived from a particular allele, for example through the *in vitro* methods discussed in 3.3.1.i and 3.3.2.i, alternative methods, such as the *in silico* methods discussed in 3.3.1.ii and 3.3.2.ii, can suggest the opposite to be true. This has shown that the BAC end sequences alone are often not sufficient to determine the allelic identity of the entire BAC and, as a result, any sequence assembled using BAC sequence data could not be assigned to either allele of the *S* locus. Therefore, in order to construct a reference sequence for this region of the *Primula* genome for the purpose of gene identification, an alternative resource should be sought.

CHAPTER FOUR

Assembly of *Primula* genomic DNA sequences

4.1 Introduction

Identifying the allelic origins of the *Blue Jeans* BACs has provided an insight into the region immediately surrounding the *Primula S* locus. This region, on the *A* side of the locus is of particular significance due to the genes that have already been identified, including the genes *PvSLL1* and *PvGLO*. It is also predicted, based on genetic mapping data, that the floral homeotic gene *sepaloid* will be found within this region, specifically between the *PvSLP1*, found in the BAC 81B15, and *PvGLO*, found in the BAC 28O8 (Li *et al*., 2008, 2008).

4.1.1 Assembly using *Blue Jeans* BAC DNA sequences

The region between *PvSLP1* and *PvGLO* also has added significance since recombinants between *PvGLO* and the *S* locus of *PvGLO* have been identified, whereas there are no known recombinants for *PvSLP1*. Whilst *PvSLP1*, unique to the *Blue Jeans* cultivar, is specific to Thrum, the gene *PvGLO* possesses both Pin and Thrum alleles, suggesting that the mechanism inhibiting recombination of the *S* locus breaks down within this region. Previous investigations into the recombination frequency of *PvGLO* have calculated the genetic distance between the *S* locus and *PvGLO* to be between 0.39 cM and 1.53 cM, though a reliable estimate for the physical distance between the two markers has not been obtained (Webster, 2005; Li *et al*., submitted). However, if a single contiguous sequence can be constructed for this region, it would be possible to reliably measure the physical distance between

these important *S* locus markers. Further to this, a complete sequence could be analysed to identify other genes, such as *sepaloid*, that may be within this region.

Sequences from the end of each BAC within the *Blue Jeans* library have already been used to position each BAC relative to each other, though these sequences themselves only cover a small fraction of the genome within this region. Although sequencing each individual BAC within the library would provide all of the sequence data necessary to construct a contig spanning this entire region, this would be costly and, due to the overlap between BACs, would produce a large amount of redundant sequence data. However, as can be seen in Figure 4.1, it is possible to link the two markers with just the four BACs 81B15, 46P3, 9B24 and 28O8, which overlap sufficiently to form an unbroken sequence between them.

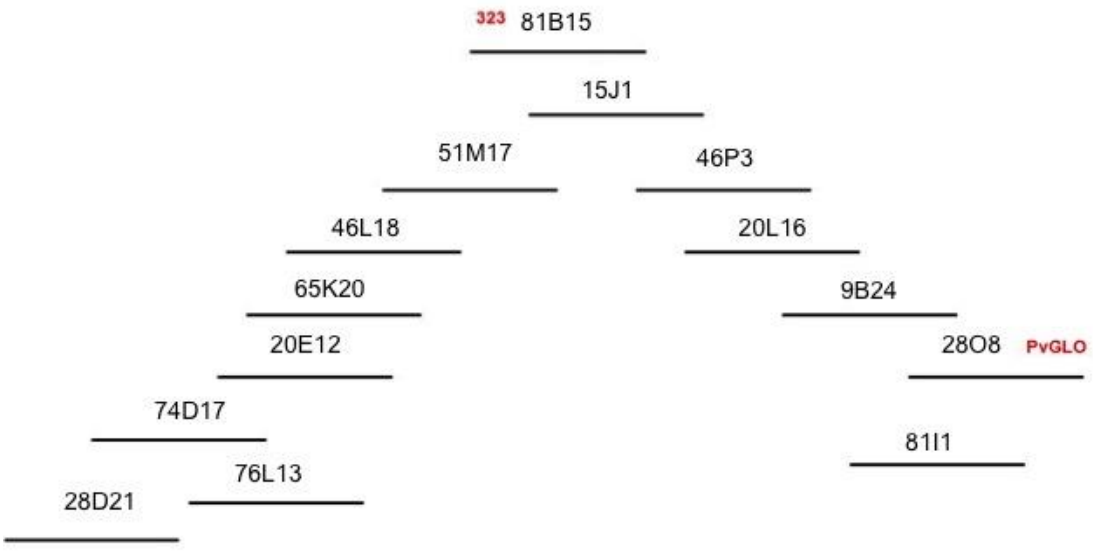


Figure 4.1: The relative positions of 14 BACs cloned from *Primula vulgaris* surrounding *PvSLP1* and *PvGLO*.

4.1.2. Assembly using wild type genomic DNA sequences

Though the single contig that could be derived from these four BACs 81B15, 46P3, 9B24 and 28O8 would form a single link between the two markers, the assignment of the *Blue Jeans* BACs, see 3.2, to different alleles of the *S* locus showed that the *Blue Jeans* BAC library contained a mix of Pin and Thrum DNA. As a result, these BAC sequences alone cannot be used to reliably characterise the genes within this area, as any genes identified could not be confidently assigned to either allele. In order to do this, the assembly of another contig, comprising DNA from a single individual of known genotype and covering the same region is necessary. Similarly, it is possible that differences exist within this region between the *Blue Jeans* cultivar, from which the BACs are derived, and the wild type *Primula vulgaris.*

While both forms of *Primula* would be suitable for use in construction of a genomic DNA contig, the heterozygous genotype of Thrum individuals would make any sequencing less reliable as the allelic origin of any sequence data would be unknown. In contrast, although the *S* locus prevents a self-crossed homozygous Pin individual from setting seed, a Pin individual would be homozygous for the Pin allele of the *S* locus. As such, all sequence data could be reliably attributed to the Pin allele, if not classified as Pin specific. In addition to this, whilst the assembly of a genomic DNA sequence using data from a single individual would generate a consistent sequence, other Pin individuals could also be used to help in the assembly. Despite SNPs or other polymorphisms that may exist between individuals, the limited recombination of the Pin allele itself means a reliable sequence can still be constructed for the purpose of gene identification. Finally, the use of wild type *Primula vulgaris* individuals for whole genome sequencing provides the opportunity to translate the knowledge already gained from studies of the *Blue Jeans* cultivar to a

more suitable system. Due to its history as a cultivated garden variety, the *Blue Jeans* genome is no longer a true reflection of the wild type as a result of various artificial selection events. Similarly, the cultivar has historically been bred through crosses with other closely related species such as *P. veris* and *P. elatior*. As a result, *Blue Jeans* individuals possess genes that would not be found in a wild type plant. Therefore, by choosing a wild type *P. vulgaris* sample for sequencing, any future work, such as that being described in this chapter, as well as Chapter 5, will serve to produce a more accurate representation of the species' 480 Mb genome.

Though the region between *PvSLP1* and *PvGLO* remains an area of particular interest, whole genome sequencing, necessary to produce the Pin genomic DNA sequence needed, would also aid in the characterisation of the region between the *PvSLP1* and *PvSLL1*. Specific Pin and Thrum alleles of *PvSLL1* have been characterised (Li *et al.,* 2007) and these are protected from recombination by the same mechanism that protects the *S* locus. Therefore, assembly of a single sequence linking this marker to *PvGLO* would further clarify the physical distance between the *S* locus and the closest gene known to recombine with it. In addition to this, a sequence linking *PvSLL1* to *PvGLO* would enable the identification of more genes that are situated close to the *S* locus.

Although whole genome sequencing of Pin individuals will provide a large amount of sequence data, it will be necessary to identify the contigs derived from this specific area of the genome. Additionally, although the sequencing process will included an automated assembly of these contigs, a higher resolution of sequence, necessary if all genes are to be identified, can be attained by manual assembly of contigs into larger sequences, as an automated assembly is likely to contain gaps. Whilst the assembled BACs from the region between *PvSLP1* and *PvGLO* will

provide a suitable scaffold for the assembly of genomic data, and alternative must be found for other regions not covered by the BAC sequence. For this purpose, the automated scaffold produced upon sequencing can be used to identify original genomic contigs and to aid in the positioning of these relative to each other. Similarly, sequence data from a self-fertilised, homozygous Long Homostyle individual, to be sequenced at the same time as the focus of a genome sequencing project, can also be used in the attempt produce a single sequence contig that will connect the molecular markers on this side of the *S* locus.

4.2 Results

4.2.1 Construction of a BAC Reference Scaffold

The four BACS 81B15, 46P3, 9B24 and 28O8 were sequenced by The Centre for Genomic Research at Liverpool University using the Roche 454 method. Sequence data was returned in the FASTA format with each BAC divided into a series of contigs. All BAC contigs referred to can be found in the 'BAC_contigs' database of the TGAC *Primula* browser.

The construction of a full BAC scaffold between the genetic marker 323 (in 81B15) and the gene *PvGLO* (in 28O8) was approached by assembling each BAC in turn before the four BACS were combined to create a single contiguous sequence. The first BAC assembled was 81B15, using the known BAC end sequences, described in 3.1, to identify the end 81B1_contig1 and 81B15_contig5 as the two end contigs for this BAC. The BAC end sequences were also used to determine the orientation of the two end contigs. For example, the orientation of 81B15.R found within

81B15_contig5 indicating that contig needed to be reverse complemented to ensure the assembled sequence would be derived from the same strand of DNA.

After the identification of the 81B15_contig1 as the 5' end contig of 81B15, the NCBI blast2n tool was used to identify other contigs that overlapped with this sequence. Using 81B15_contig1 as a query and the remaining contigs as subjects, a blast2n search showed that 81B15_contig11 shared 2,135 bases in common at the 3' end of 81B15_contig1. As a result, these two contigs could be assembled by removing the overlapping sequence from 81B15_contig11 and joining the sequence to 81B15_contig1.

The same procedure was used to subsequently joining 81B15_contig7 to the newly assembled sequence. In this instance, blast2n analysis revealed that the sequence provided for 81B15_contig7 was in the opposite orientation to the joined 81B15_contigs 1 and 11. As such, the reverse complement sequence of 81B1_contig7 was used to extend the BAC sequence. Similarly, the NCBI blast2n tool was also to join the reverse complements of 81B15_contigs 4, 2 and 3 to the 5' end of 81B15_contig5, already known to be the end contig at the 3' end of the BAC.

Following the assembly of the 2 sequences, each extending from the BAC ends, 81B1_contig9 remained as the only contig not yet incorporated into the assembly. However, no overlap between this contig and either 81B15_contig7 or 81B1_contig4 could be identified. As a result, 81B15_contig9 could not be orientated within this gap using the same method.

In order to complete the assembly of the 81B15 BAC sequence, primers were designed from both ends of 81B15_contig9 as well as from the ends of 81B15_contig7 and 81B15_contig4 and PCR was used to identify the orientation of this contig. Sequencing of PCR products in a preliminary analysis of the region also

revealed that both ends of 81B15_contig9 were immediately adjacent those of 81B15_contig7 and 81B15_contig4. These findings were confirmed and the contig was therefore used to join the two sequence assemblies together and complete the BAC sequence. Details of the primers are shown in Appendix A. The final order of these contigs within 81B15 can be seed in Figure 4.2.

As described above, each of the four BAC sequences was assembled individually and the same process was used in each instance. In order to assemble the four separate BACs into a single contiguous sequence, the same process was used. Using the NSBI blast2n tool and treating each BAC as a separate sequence, overlaps between the four separate BACs were identified. Any duplications in sequence between BACs was removed that the sequences were joined to form a single contiguous sequence 183,331bp in length.

Table 4.1 shows the order of each BAC contig within the assembled BAC reference scaffold as well as their lengths and orientations. Table 4.1 also shows that a total of 39,025 bases were removed from the assembled sequences when overlaps were removed. Table 4.1 also details the orientations of the original BAC contig sequences once incorporated into the scaffold. The symbol +/+ indicates that contig sequences were already in the correct orientation for assembly whereas +/- indicates that the reverse complement of the contig sequence was used. These data are also represented diagrammatically in Figure 4.2, which shows the relative position of each BAC contig within the assembled scaffold. Figure 4.2 also demonstrates how, despite the cumulative length of the contigs exceeding that of the assembled scaffold, the assembled length is less than this, once the overlaps between each BAC contig have been taken into consideration.

BAC Contig	Orientation	BAC Contig Length (bp)	Cumulative Sequence Length (bp)
81B15_contig1	**+/+**	**8518**	**8518**
81B15_contig11	**+/+**	**4643**	**13161**
81B15_contig7	**+/-**	**11482**	**24643**
81B15_contig9	**+/+**	**3886**	**28529**
81B15_contig4	**+/-**	**9426**	**37955**
81B15_contig2	**+/-**	**2912**	**40867**
81B15_contig3	**+/-**	**476**	**41343**
81B15_contig5	**+/-**	**2852**	**44195**
46P3_contig2	**+/-**	**12456**	**56651**
46P3_contig7	**+/+**	**10115**	**66766**
46P3_contig11	**+/+**	**384**	**67150**
46P3_contig6	**+/+**	**453**	**67603**
46P3_contig4	**+/+**	**543**	**68146**
46P3_contig1	**+/+**	**20906**	**89052**
9B24_contig13	**+/+**	**2375**	**91427**
9B24_contig1	**+/-**	**2503**	**93930**
9B24_contig3	**+/+**	**30372**	**124302**
9B24_contig11	**+/+**	**5273**	**129575**
9B24_contig10	**+/-**	**21068**	**150643**
28O8_contig2	**+/+**	**3295**	**153938**
28O8_contig1	**+/-**	**29111**	**183049**
28O8_contig9	**+/+**	**9375**	**192424**
28O8_contig11	**+/+**	**2267**	**194691**
28O8_contig7	**+/-**	**730**	**195421**
28O8_contig3	**+/-**	**5731**	**201152**
28O8_contig4	**+/-**	**14393**	**215545**
28O8_contig6	**+/-**	**6811**	**222356**
Assembled Contig Length			**183331bp**

Table 4.1: The BAC contigs used in the assembly of the *Blue Jeans* BAC reference scaffold. Contigs are shown in order from 5’ to 3’.

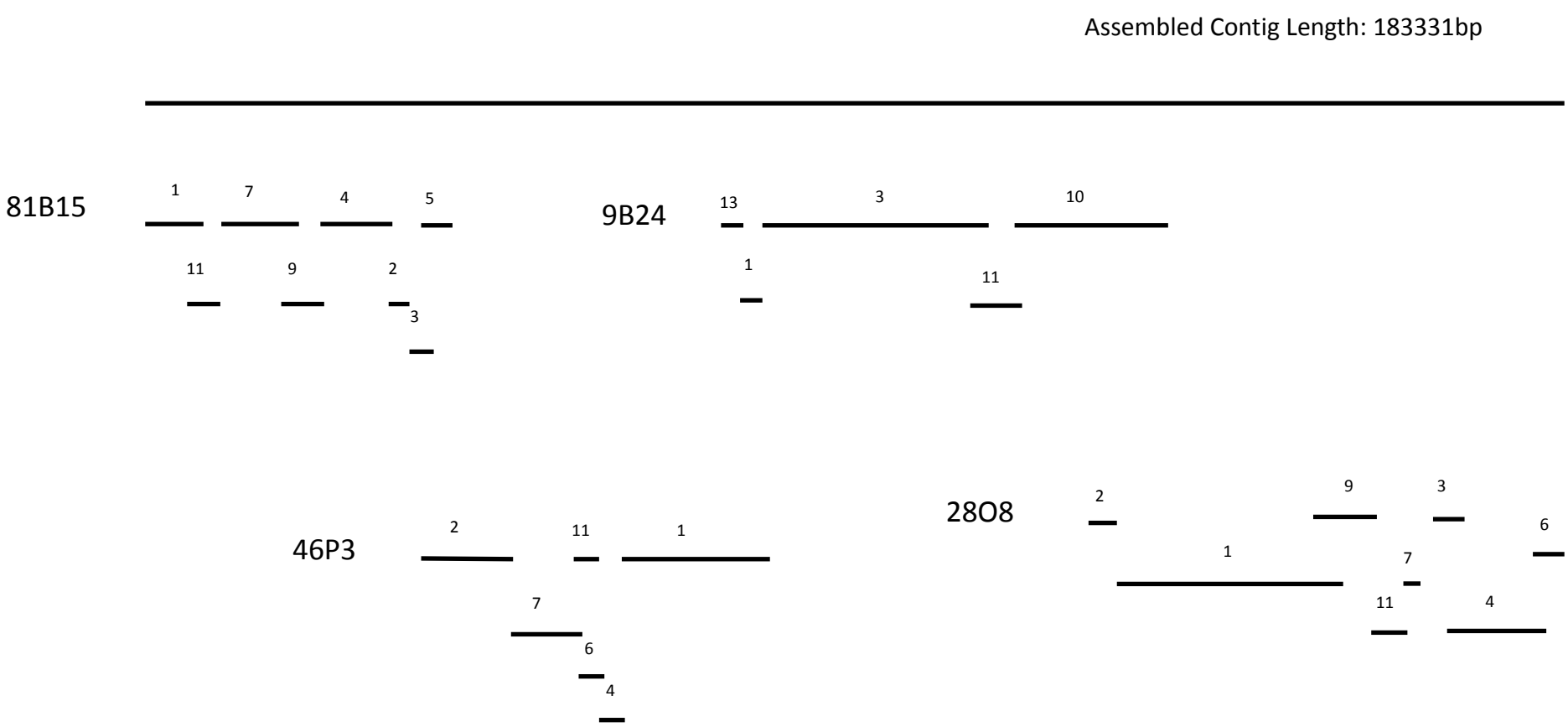


Figure 4.2: Sequence overlap diagram of the *Blue Jeans* BAC Reference scaffold. Relative positions of the contigs of 81B15, 46P3, 9B24 and 28O8 sequence contigs are shown. Identity of each contig is given.

4.2.2 Assembly of *Primula vulgaris* genomic DNA sequence

Assembly of a sequence comprising solely genomic DNA from a Wild Type Pin individual took place in two steps. The first of these was the conversion of the existing BAC scaffold, described in 4.2.1, from *Blue Jeans* BAC DNA into wild type genomic DNA using sequence data from a wild type Pin individual. Following this, the genomic DNA sequence could be extended further using the available sequence data.

Genomic DNA from a wild type Pin individual was sequenced by The Genome Analysis Centre using the Illumina sequencing method. In addition to this, a pool of genomic DNA, extracted from the Pin progeny of the first individual, and genomic DNA from a long homostyle individual were also sequenced. All contigs referred to can be found in the TGAC *Primula* browser in the following databases:

- pin_pnt_wgs_ab_71_ contigs can be found in the prim-pinparent-k71-scaffolds database, subsequently referred to as the Parent Database.
- pin_pl_wgs_ab_71_ contigs can be found in the prim-pinpool-k71-scaffolds database, subsequently referred to as the Progeny Database.
- longhomo_wgs_ab_81_ contigs can be found in the prim-longhomo-k1-scaffolds database, subsequently referred to as the Long Homostyle Database.
- Pin_pnt_scaffold contigs can be found the prim-pinparent-ab-ctg-scaff database, subsequently referred to as the Pin Scaffold Database.

When possible, contigs from the original Parent Database were used in order to maintain consistency. All contigs that formed part of the genomic DNA sequence can be seen in Table 4.2.

4.2.2.i Conversion of the BAC Scaffold to Pin genomic DNA

To convert the previously assembled BAC Reference Scaffold, see 4.2.1, into Pin genomic DNA, the complete scaffold sequence was used in a BLAST search of the prim-pinparent-k71-scaffolds database. This search identified 10 large genomic DNA contigs that each matched to different regions of the BAC scaffold. In order to maintain the integrity and reliability of the assembled sequence data, only sequences with an identity over 90% were recorded.

The 1st large contig identified was pin_pnt_wgs_ab_71_3858690, a contig 35,649bp in length that matched the first 5,528 bases of the BAC scaffold and extended the sequence by 30,121 bases. Similarly, the 10th contig, pin_pnt_wgs_ab_71_3787655, a sequence 28,236bp in length, matched to the last 6834bp of the BAC reference scaffold and therefore extended the sequence by 21413bp.

Although some of these large contigs already overlapped with each other and could be joined immediately, a number of them were separated by gaps. For example, a gap of 23,343bp existed between the first contig pin_pnt_wgs_ab_71_3858690 and pin_pnt_wgs_ab_71_3711669, the next of the 10 large genomic contigs identified by the initial BLAST search. In order to close this gap, pin_pnt_wgs_ab_71_3858690 was used as a query to search both the Parent Database and the Progeny Database. This search identified the contig pin_pl_wgs_ab_71_4625639, which was in turn used to identify pin_pl_wgs_ab_71_4450338 in a similar BLAST search, extending the sequence further into the gap between the two original contigs. A further BLAST search using pin_pl_wgs_ab_71_4450338 as a query identified the contig pin_pnt_wgs_ab_71_3750481, a sequence that also overlapped with the large contig pin_pnt_wgs_ab_71_3711669 and closed the gap between the two original large contigs.

This same process was used to complete any other gaps between the large contigs identified by the original BLAST search. Two exceptions to this occurred between contigs pin_pnt_wgs_ab_71_3687878 and pin_pnt_wgs_ab_71_3688273 as well as pin_pnt_wgs_ab_71_3745308 and pin_pnt_wgs_ab_71_3849147. In these instances, both contigs were extended towards each other in the method described though no match could be found to close the gap between two sequences. Therefore, a number of Ns were inserted to join the sequences according to the size of the gap, determined using the BAC reference scaffold. However, with the exceptions of these two small regions, the BAC Reference Scaffold was successfully converted to wild type Pin genomic DNA, producing a single contiguous sequence that linked *PvSLP1* to *PvGLO*.

4.2.2.ii Extension of genomic DNA sequences

The availability of new genomic DNA sequence data also allowed for the extension of the converted BAC Reference scaffold towards *PvSLL1*. In order to identify genomic DNA contigs from the region surrounding this gene, the genomic sequence of *PvSLL1* was used as a query and identified the contig pin_pnt_wgs_ab_71_3847249.

Using the same technique described in 4.2.2.i, this contig was used to identify other contigs within both the Parent and Progeny Databases in order to identify neighbouring contigs. In addition to this, contig pin_pnt_wgs_ab_71_3847249 was also used to search the Long Homostyle Database and the Pin Scaffold Database. Although contigs identified in these two databases did not form part of the assembled sequence, they were used as references when overlapping sequences could not be identified. An example of this is the extension of the contig

pin_pnt_wgs_ab_71_3847249, identified using *PvSLL1*, in the 5' direction. Though no overlapping sequence could be found within either Parent or Progeny Datbases, the scaffold pin_pnt_scaffold4032 was identified within the Pin Scaffold Database. This pre-existing scaffold sequence was then used to identify the Parent contig pin_pnt_wgs_ab_71_3714983 located 2011 bases from the 5' end of pin_pnt_wgs_ab_71_3847249. Though the scaffold sequence gave no indication as to the sequence between the two contigs, it gave an indication of size and the two contigs were joined by Ns.

The sequence surrounding *PvSLL1* was also extended towards *PvGLO* using the same process until no more overlapping contigs could be identified to further extend the sequence surrounding *PvGLO*, resulting in a sequence 126,215bp long. In order to identify new genomic contigs in the region between the two assembled sequences, *Blue Jeans* BACs from the region were identified and their end sequences were used to BLAST the Parent Database. Using the BAC end sequence from the R end of BAC 20E12, the contig pin_pnt_wgs_ab_71_3805517 was identified and used to identify further contigs from the surrounding area within the Parent and Progeny databases. This process was repeated and led to the identification of 19 contigs that formed a single sequence 106,288bp in length. Of these 19 contigs, only 2 (pin_pl_wgs_ab_71_4412622 and pin_pnt_wgs_ab_71_ 3803757) were found not to overlap. In order to join these contigs together, pin_pl_wgs_ab_71_4412622 was used to search the Long Homostyle database and identified the contig longhomo_wgs_ab_81_889015. When this sequence was then used to search the Parent Database, the contig pin_pnt_wgs_ab_71_3803757 was found 443 bases from the 3' end of the first contig. Due to the nature of the Long Homostyle sequence, it could not be confirmed that the sequence between these two contigs would be the

same within the Pin genome. As such, the sequence between the two contigs was replaced with Ns.

Once the contig around 20E12 could not be extended any further, it could be seen that a gap remained between this contig and that surrounding *PvSLL1*. As a result, the first sequence (around *PvSLL1*) was named Seq1 and the second sequence (around 20E12) was named Seq2.

Similarly, a gap also remained between Seq2 and the assembled sequence surrounding *PvGLO*. Therefore, the same approach was used to identify new sequence between these two sequences. The BAC 51M17 was identified within this region and the F end sequence was used to isolate the genomic contig pin_pnt_wgs_ab_71_3858690. This sequence was then extended in both directions, using both Parent and Progeny Databases as well as the Pin Scaffold Database for reference, until it could be extended no more in the 5' direction and joined to the existing sequence around *PvGLO* in the 3' direction. As a gap still remained between this sequence and Seq2, this contig was designated Seq3 and had a total length of 277,924bp. Seq1, Seq2 and Seq3, and the positions of *PvSLL1*, *PvSLP1* and *PvGLO* are represented in Figure 4.2.

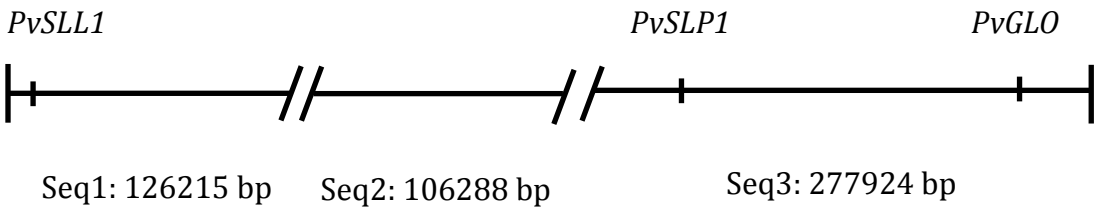


Figure 4.3 Sizes and relative positions of Seq1, Seq2 and Seq3. Positions of the markers *PvSLL1*, *PvSLP1* and *PvGLO* are shown.

Table 4.2 shows the order of the Pin genomic DNA contigs within the three assembled contigs, as well as their lengths and orientations. Table 4.2 also shows the cumulative length of the combined contigs in each sequence, as well as the assembled sequence length once overlaps between contigs had been removed.

Although the three contigs shown in Table 4.2 remained as three separate sequences, known BAC end sequences were identified near the ends of each sequence. This included end sequences from the same BAC found in different sequences. As such, the estimated BAC sizes suggested that a large distance could not exist between contigs. Therefore, the three contigs were provisionally joined together, using the code XXX to signify the breaks between Seq1, Seq2 and Seq3. This completed sequence can be seen in Appendix B. Figure 4.4 shows the relative positions of each of the contigs listed in Table 4.2 within Seq1, Seq2 and Seq3. As shown in Figure 4.4, the cumulative length of all of the contigs included would far exceed the length of each sequence. However, as in Figure 4.2, the assembled length of each sequence is reduced when overlaps between each contig is taken into account.

Genome Contig	**Orientation**	**Contig Length (bp)**	**Cumulative Sequence Length (bp)**
Seq1			
pin_pnt_wgs_ab_71_36742587	**+/-**	**9428**	**9428**
pin_pl_wgs_ab_71_4575578	**+/+**	**2741**	**12169**
N		**187**	**12356**
pin_pnt_wgs_ab_71_3714983	**+/+**	**8533**	**20889**
N		**2011**	**22900**
pin_pnt_wgs_ab_71_3847249	**+/+**	**35226**	**58126**
pin_pl_wgs_ab_71_4635008	**+/+**	**6491**	**64617**

N		**1187**	**65804**
pin_pnt_wgs_ab_71_330645	**+/+**	**34562**	**100366**
pin_pnt_wgs_ab_71_3846419	**+/-**	**33242**	**133608**
Assembled Contig Length			**126215 bp**
Seq2			
pin_pnt_wgs_ab_71_3803370	**+/-**	**3435**	**3435**
pin_pnt_wgs_ab_71_ 3803369	**+/+**	**7863**	**11298**
pin_pnt_wgs_ab_71_ 3826434	**+/-**	**10636**	**21934**
pin_pnt_wgs_ab_71_ 3852102	**+/-**	**5210**	**27144**
pin_pnt_wgs_ab_71_ 3802165	**+/-**	**5091**	**32235**
pin_pnt_wgs_ab_71_ 3809657	**+/-**	**23493**	**55728**
pin_pnt_wgs_ab_71_ 3858100	**+/-**	**4084**	**59812**
pin_pnt_wgs_ab_71_ 3805517	**+/-**	**26861**	**86673**
pin_pl_wgs_ab_71_4628703	**+/+**	**35297**	**121970**
pin_pnt_wgs_ab_71_ 3710618	**+/+**	**3298**	**124268**
pin_pl_wgs_ab_71_4412622	**+/+**	**1759**	**127027**
N		**443**	**127470**
pin_pnt_wgs_ab_71_ 3803757	**+/-**	**1048**	**128518**
pin_pnt_wgs_ab_71_ 3791730	**+/-**	**2387**	**130905**
pin_pnt_wgs_ab_71_ 3791733	**+/**	**3914**	**134819**
pin_pnt_wgs_ab_71_ 3804125	**+/**	**9894**	**144713**
pin_pnt_wgs_ab_71_ 3854238	**+/**	**15357**	**160070**
pin_pnt_wgs_ab_71_ 3688763	**+/**	**4030**	**164100**
Assembled Contig Length			**106288bp**
Seq3			
pin_pl_wgs_ab_71_4638286	**+/+**	**8065**	**8065**
pin_pnt_wgs_ab_71_ 3721676	**+/+**	**7731**	**15796**
pin_pl_wgs_ab_71_ 4431548	**+/+**	**1791**	**17587**
N		**491**	**18078**
pin_pnt_wgs_ab_71_ 3830600	**+/+**	**31239**	**49317**
N		**134**	**49451**
pin_pnt_wgs_ab_71_3858690	**+/+**	**35649**	**85100**
pin_pl_wgs_ab_71_4625639	**+/-**	**1688**	**86788**
pin_pl_wgs_ab_71_4450338	**+/**	**572**	**87360**
pin_pnt_wgs_ab_71_3750481	**+/+**	**10578**	**97938**

pin_pnt_wgs_ab_71_371669	**+/-**	**24012**	**121950**
pin_pnt_wgs_ab_71_3687878	**+/+**	**12124**	**134074**
N		**13**	**134087**
pin_pnt_wgs_ab_71_3688273	**+/-**	**8454**	**142541**
pin_pnt_wgs_ab_71_3691095	**+/-**	**8233**	**150774**
pin_pnt_wgs_ab_71_3687726	**+/+**	**10454**	**161228**
pin_pnt_wgs_ab_71_3741541	**+/+**	**9168**	**170396**
pin_pl_wgs_ab_71_4426546	**+/-**	**4827**	**175223**
pin_pnt_wgs_ab_71_3850227	**+/-**	**4497**	**179720**
pin_pl_wgs_ab_71_4434231	**+/-**	**4018**	**183738**
pin_pnt_wgs_ab_71_3844744	**+/+**	**29925**	**213663**
pin_pl_wgs_ab_71_4597131	**+/+**	**23452**	**237115**
pin_pnt_wgs_ab_71_3745308	**+/-**	**7217**	**244332**
N		**132**	**244464**
pin_pnt_wgs_ab_71_3849147	**+/+**	**6143**	**250607**
pin_pnt_wgs_ab_71_3688236	**+/+**	**9145**	**259752**
pin_pl_wgs_ab_71_4622992	**+/+**	**32926**	**292678**
pin_pnt_wgs_ab_71_3787655	**+/+**	**28236**	**320914**
Assembled Contig Length			**277924 bp**

Table 4.2: Pin genomic DNA contigs used to assemble Seq1, Seq2 and Seq3. Contigs are shown in order from 5’ to 3’. N indicates are series of Ns inserted into the sequence.

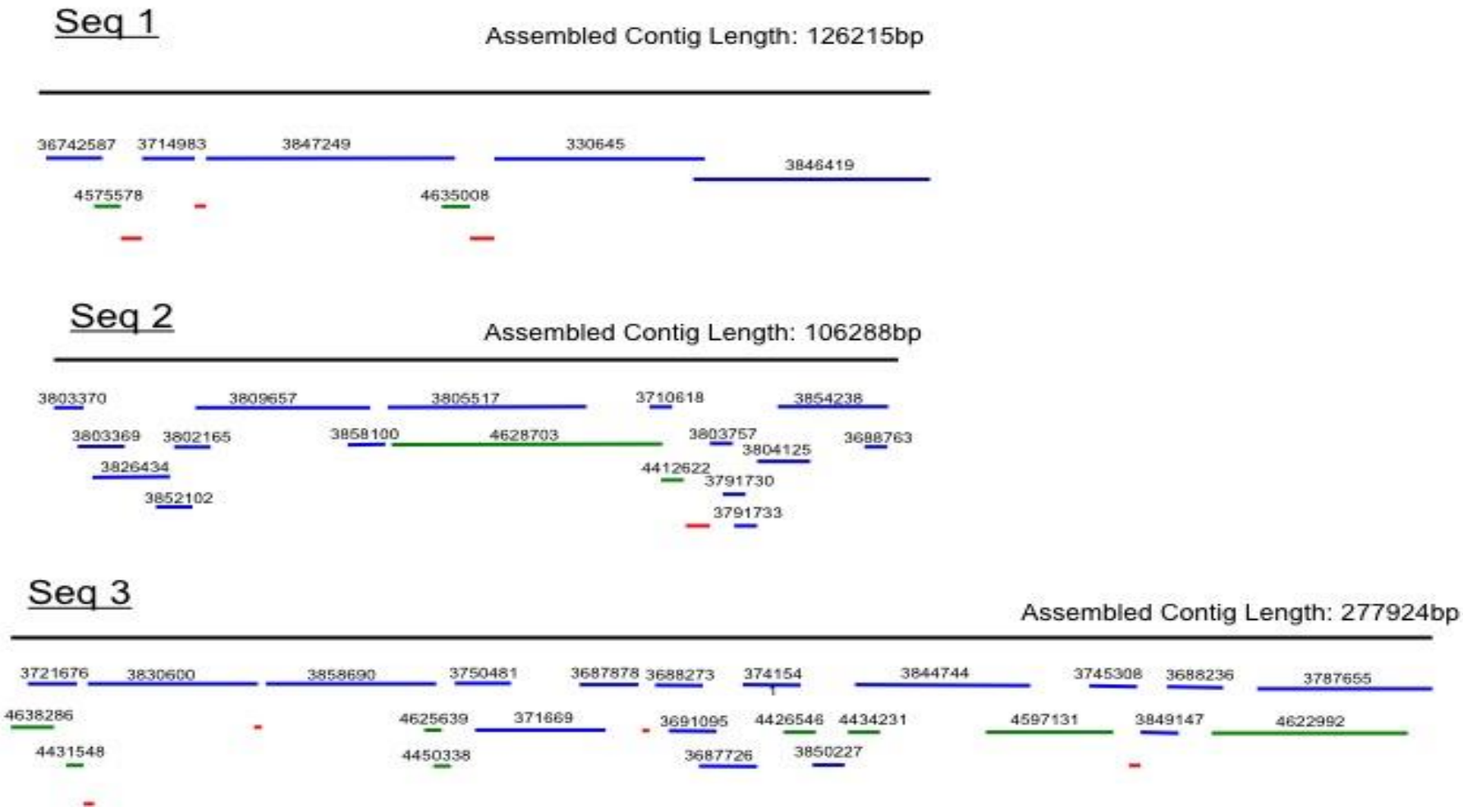


Figure 4.4 Sequence diagrams of Seq1, Seq2 and Seq3. Relative positions of contigs within each sequence are shown, including overlaps between sequences. Blue bars signify contigs form the Parent Database and green bars signify contigs from the Progeny Database. Red bars represent sequences of Ns. Numbers above each bar denotes the identity of each contig.

4.3 Discussion

The assembly of the three contigs of genomic DNA sequence described in this chapter is significant for a number of reasons. First among these is the breakdown of the mechanism that prevents recombination within the *S* locus that occurs within this region. Although *PvSLL1*, found near the 5' end of Seq1, is tightly linked to the *S* locus, with only one potential recombination ever seen, *PvGLO*, found near the 3' end of Seq3, is known to recombine much more frequently. As such, the mechanism that restricts recombination of the *S* locus itself must be lost between these two genes. The secondary significance of these contigs is that they make it possible, for the first time, to measure the physical distance between the previously characterised *S* locus markers.

Assembly of the contigs themselves was successful. In particular, the assembly of the largest contig, Seq3, was reliant on the construction of the BAC Reference Scaffold assembled using *Blue Jeans* BAC DNA. Although this sequence was complete in itself, the decision to incorporate a number of Ns into the sequence upon conversion to Pin genomic DNA, see 4.2.2.i, introduces the possibility that some important genetic data have been lost from the genomic DNA sequence. However, this is unlikely given the relatively small number of Ns that were inserted into the sequence. In addition to this, though it was desirable to convert as much of the BAC Reference Scaffold as possible into genomic sequence, it was also important to ensure that only Pin genomic sequence was used. However, as demonstrated in Chapter 3, although the BAC 81B15 was derived from a single allele of the locus, other BACS further from the *S* locus, such as 28O8, appeared to have recombined, possessing elements from both alleles. As such, the data from the BAC reference

scaffold could not be reliably used to close the gap and maintain the integrity of a Pin specific assembly.

Two further sources of reference sequence were also available when attempting to close gaps between contigs in the Seq1, Seq2 and Seq3 assemblies for use as an alternative scaffold. The first of these was Long Homostyle genome data. As a result of the self-incompatibility of wild type Pin individuals, natural variation outside of the immediate *S* locus region limited the length of the reads produced during Illumina sequencing. However, as self-fertile mutants, Long Homostyle individuals could be used to produce inbred progeny, with a reduced level of variation in the area surrounding G, P and A. As such, when sequencing these individuals, less variation was seen between individual reads and they could be more easily assembled into longer contigs. By using the Long Homostyle data as an alternative scaffold, the chances of identifying an overlapping sequence from either the Parent or Progeny was therefore increased and new contigs could be identified to extend the assembled sequences. Once new Parent or Progeny contigs had been identified, however, any remaining Long Homostyle sequence data that could not be directly replaced with data from wither of the Pin databases was removed and replaced with Ns. As discussed above, in 4.1.2, efforts were made to assemble as much of the sequence as possible from the genome data of a single Pin individual or, if this was not possible, its Pin progeny. In order to maintain the integrity of the assembled sequence as 'Pin only' therefore, it was necessary to removed any sequences such as these that could not be confidently assigned to the Pin genome and not the Thrum.

The other reference sequences used were the Pin Scaffold sequences, assembled automatically by TGAC upon sequencing. Similar to the Long Homostyle contigs, these sequences provided a longer reference sequence than the Parent or Progeny

contigs but did not offer the same resolution of sequence as a manual assembly using Pin Parent contigs alone. In addition to this, repeated attempts to combine Parent contigs into a scaffold automatically meant that the scaffold sequences available were updated regularly, and could have led to an erroneous or obsolete assembly. Unlike the Long Homostyle contigs used as reference sequences however, these Pin Scaffold contigs were unable to provide sequence data to fill gaps that remained between assembled contigs, instead only giving indications of size. As such, Ns were used to fill these gaps.

The final assembly of genomic DNA contigs resulted in three large sequences, collectively spanning 510,427bp. However, although these sequences remained three separate contigs, the presence of BAC end sequences from the same BACs in two different contigs made it possible to estimate the maximum possible distance between each contig. At the time that this research was completed, the sequence data to complete the gaps between Seq1, Seq2 and Seq3 was unavailable and the decision was made to combine the three sequences together with a clear indication (XXX) of where the junctions between contigs were. This was made in order that the sequence could be completed when more sequence data was available. While the possibility remained that important genetic data was lost with the premature joining of the three contigs, the estimated BAC sizes suggested that such a loss should remain minimal and, by clearly marking the joins between contigs, these regions could be easily revisited in the future.

The combination of Seq1, Seq2 and Seq3 into a single assembled genomic DNA contig provides a physical link between the two *S* locus markers *PvSLL1* and *PvGLO*. However, whilst these two genes have been previously identified and characterised, the assembly of the genomic DNA sequence described in this chapter

now also allows for the identification of any other genes that may exist within this region.

CHAPTER FIVE

Identification and annotation of *Primula vulgaris* genes

5.1 Introduction

The functions of the *Primula vulgaris S* locus have been known since Ernst (Ernst 1933, 1936b, 1955) identified the three genes that comprise the locus. However, the area immediately surrounding this area, and the genes contained within it, has remained largely uncharacterised. While more recent work has identified genes such as *PvSLL1* and *PvGLO*, which are linked to the *S* locus (Li *et al.*, 2007, 2008), these genes have been used largely as markers for the locus itself and the region of genome between them has been subject to little analysis. As such, the assembly of a sequence that links these two genes provides an opportunity to identify other genes in this area.

In Chapter 4, three sequences were assembled using genomic DNA from a wild type Pin individual and are known to collectively span the distance (over 500kb) between *SLL1* and *PvGLO*. Although these contigs remain separate sequences, the method by which they were assembled, using BAC sequences as a scaffold, makes it possible to position each sequence relative to the remaining two whilst maintaining a good idea of the distances between the ends of each contig. While the separate nature of the contigs must be born in mind, it is possible, therefore, to join the three sequences together to form a single consecutive sequence 510,427bp in length for the purpose of identifying genes. This complete sequence can be seen in Appendix B, in which the symbol XXX has been used to signifying breaks between contigs.

With the construction of a single sequence containing both genetic markers *SLL1* and *PvGLO*, it is now possible to analyse the area for any other genes by identifying

homology between the *Primula* genomic sequence and the known sequences of genes from other species.

5.2 Results

5.2.1 Identification of *Primula vulgaris* genes

Genes were identified within the assembled *Primula vulgaris* sequence using the NCBI BLASTX tool. However, the size of the assembled sequence (510,427 bp) presented a problem as it was too large to be analysed in a single BLASTX search. As such, sequence was split into a total of 57 smaller contigs. This was done by dividing the sequences into 10Kb sub-contigs, with each sub-contig overlapping by 1Kb to minimise the risk of missing genes located across the boundaries between sub-contigs.

Table 5.1 shows details of the genes that were identified within the assembled sequence. 51 genes were identified within the sequence. Each gene was assigned a number, *PvG1 – PvG51*, and its position within the whole assembled sequences was calculated. As can be seen in Table 5.1, NCBI BLAST suggests a variety of functions, among which were *PvSLL1* (labelled as *PvG2*) and *PvGLO* (*PvG49*). The column on the far right of Table 5.1 shows the regions of the subject sequence that were identified by the *Primula* query in the BLASTX search. Although some genes, such as *PvG1*, only identified a single region from the subject, in this instance a *Medicago truncatula* ARS binding protein, other genes, such as *PvG24*, which matched to an uncharacterised protein from *Zea mays* but with a suggested function as a chaperonin protein, identified 12 smaller regions within its subject that combined to cover the entire gene. Therefore, it was assumed that each region of

matching sequence represented an exon. Table 5.1 shows a range of scores and E-values for the different matches that were seen.

A number of the genes identified within Table 5.1 are of particular interest. 3 of the genes identified (*PvG15, PvG25, PvG34*) found matches to hypothetical proteins from *Vitis vinifera* and a further 7 (*PvG11, PvG17, PvG19, PvG22, PvG24, PvG30, PvG47*) found matches to proteins that are as yet uncharacterised in their relevant species. Another 2 genes of note are *PvG9* and *PvG10*. Found next to each other and with the same suggested identity; both match to the same regions of a *Populus trichocarpa* Cytochrome P450 protein. *PvG23* also displays an interesting pattern in its match to a Pentatrichopeptide-repeat containing protein from *Vitis vinifera*, with a number of regions from the query sequence matching to the same region from the same subject. A final gene of note is *PvG46*, a match to the *Petunia x hybrid* MADS-box protein *FBP24*.

Gene #	Accession #	Identity	Subject Species	Score	E-Value	Query Location	Matching Subject Sequence
PvG1	XP_003617045.1	ARS Binding Protein	*Medicago truncatula*	50.8	0.007	5261-5374	177-2147
PvG2	ABD78323.1	SLL1 Protein	*Primula vulgaris*	82	$2e^{-24}$	24444-24641	17-91
PvG3	ABA08442.1	Neutral/Alkaline Invertase	*Manihot esculenta*	191	0	31803-31510	137-459
				627	$4e^{-47}$	35276-34512	460-557
PvG4	AAD25646.1	Retroelement pol polyprotein	*Arabidopsis thaliana*	67	0	53486-53217	60-149
				613	0	53181-50296	169-1125
				247	0	50192-49443	1411-1433
				28.9	0	49440-48372	1158-1409
PvG5	EOY17232.1	Disulphide-Isomerase-like protein	*Theobroma cacao*	82.8	$4e^{-15}$	58284-58418	25-69
				57	e^{-4}	64450-64554	68-102
				200	$7e^{-51}$	64764-65135	103-226
				160	e^{-37}	65687-66025	219-330
				107	$6e^{-21}$	66406-66654	330-413
PvG6	XP_003556191.1	E3 Ubiquitin-protein ligase RNF167-like	*Glycine max*	97.4	$2e^{-17}$	72465-72238	42-116
				219	$3e^{-57}$	70398-69952	104-253
				72.8	e^{-9}	68548-68432	255-293
				77	$7e^{-11}$	68176-67922	417-495
PvG7	XP_002328508.1	Predicted Protein	*Populus trichocarpa*	392	$3e^{-199}$	80266-79379	1-299
PvG8	XP_004230120.1	Serine/threonine Protein KinaseWNK1-like	*Solanum lycopersicum*	145	$2e^{-31}$	98701-98928	39-144
				142	e^{-30}	99543-99770	114-189
				109	$9e^{-21}$	100499-100657	188-240
				129	e^{-26}	100923-101468	241-413
				16	$2e^{-37}$	101947-102372	390-529
				51.6	0.008	102545-103081	539-746
PvG9	XP_004245646.1	Cytochrome P450.1	*Populus trichocarpa*	224	e^{-58}	108425-109222	32-301
				117	e^{-56}	110418-111014	306-504

PvG10	XP_004245646.1	Cytochrome P450.1	*Populus trichocarpa*	245	$6e^{-66}$	114118-114915	32-301
				229	$2e^{-60}$	115363-115962	305-503
PvG11	EOY17225.1	Uncharacterised Protein	*Theobroma cacao*	100	e^{-19}	118053-118448	62-199
PvG12	ADE77272.1	Unknown Protein	*Picea sitchensis*	108	$4e^{-22}$	119344-119610	137-228
PvG13	AGH32908.1	Squalene Epoxidase	*Camelia oleifera*	80.1	e^{-104}	132720-132610	91-127
				206	e^{-104}	132487-132047	126-243
				146	e^{-104}	131964-131740	242-316
				170	e^{-40}	131185-130895	315-411
				69.7	$4e^{-58}$	130138-130031	499-534
				186	$4e^{-58}$	126601-126715	4007-4348
PvG14	ACB4746.1	Chalcone synthase	*Citrus sinensis*	60.1	e^{-5}	144607-144783	1-60
				248	$3e^{-155}$	145128-145706	55-246
				198	$3e^{-155}$	145706-146137	247-390
PvG15	CAN81537.1	Hypothetical Protein	*Vitis vinifera*	347	$6e^{-103}$	155050-155718	37-259
PvG16	XP_003542961.1	Long Chain Acyl-CoA synthetase 9	*Glycine max*	134	e^{-28}	162268-162549	57-150
				59.7	$2e^{-5}$	162963-163067	146-180
				137	$2e^{-29}$	163234-163545	161-265
				165	e^{-38}	163894-164310	263-368
				127	$2e^{-26}$	164673-164906	367-444
				89	2e-14	165184-165409	445-486
				89	$2e^{-63}$	165441-165584	482-529
				100	$2e^{-63}$	165661-165801	527-573
				105	$2e^{-63}$	165917-166126	572-641
				92.4	$2e^{-15}$	166478-166651	639-696
PvG17	XP_002285854.1	Uncharacterised Protein	*Vitis vinifera*	41.6	2.8	71215-71440	21-95
				73.9	0	73640-73960	96-190
PvG18	XP_004250311.1	Chlorophyllide a	*Solanum*	121	$4e^{-36}$	185489-185722	31-108

		oxygenase	*lycopersicum*	61.6	$4e^{-36}$	185820-185927	108-143
				102	$6e^{-19}$	186392-186670	142-234
				101	$2e^{-18}$	187129-187278	235-284
				124	$6e^{-26}$	187607-187804	284-349
				65.1	$4e^{-7}$	187929-188087	345-394
				207	$8e^{-53}$	188141-188458	371-482
				102	$8e^{-19}$	188824-188985	481-534
PvG19	XP_004242030.1	Uncharacterised Protein	*Solanum lycopersicum*	126	e^{-29}	190058-189573	1-105
PvG20	XP_003581684.1	Delta-aminolevulinic Acid Dehydratase	*Brachypodium distachyon*	50.1	0.016	4884-4780	112-146
				57	e^{-4}	4736-4693	125-174
				46.2	$5e^{-77}$	4002-3934	160-182
				60.5	$5e^{-77}$	3866-3771	180-211
				55.5	$5e^{-77}$	3657-3586	211-234
				85.9	$5e^{-77}$	3506-3249	234-293
				57	$5e^{-77}$	3142-3059	293-320
				58.9	$5e^{-77}$	2964-2869	325-346
				58.2	$5e^{-77}$	2777-2691	343-371
				84.3	$3e^{-13}$	2448-2296	372-422
PvG21	XP_003627109.1	Zinc Finger Protein	*Medicago truncatula*	243	$6e^{-65}$	199683-200087	70-204
				62.4	$3e^{-6}$	201024-201641	204-494
PvG22	XP_002280177.1	Uncharacterised Protein	*Vitis vinifera*	73.6	$7e^{-11}$	214666-214923	79-130
				37.4	0.001	215376-215441	127-148
				35.8	0.001	215512-215574	145-164
PvG23	CBI35955.3	Pentatricopeptide repeat containing protein	*Vitis vinifera*	250	e^{-65}	222038-221277	1-248
				47.8	0.088	220256-219759	51-255
				101	$3e^{-18}$	220646-219930	54-263
				139	$3e^{-30}$	220769-219930	117-403

				94	$9e^{-16}$	221918-221290	136-387
				553	e^{-169}	220784-219438	248-703
				98.2	$3e^{-17}$	221795-221247	347-536
PvG24	NP_001140224.1	Uncharacterised Chaperonin Protien	*Zea mays*	51.6	0.004	229442-229332	8-44
				100	e^{-58}	228771-228487	44-110
				47.8	e^{-58}	228379-228293	111-139
				52.4	e^{-58}	228188-228078	134-170
				55.5	e^{-58}	228012-227911	168-201
				41.6	e^{-58}	227825-227751	196-223
				41.2	e^{-58}	227688-227605	219-246
				57	$8e^{-5}$	227189-227082	243-278
				59.3	$6e^{-14}$	226616-226524	281-311
				48.5	$6e^{-14}$	226450-226328	311-349
				52.8	0.002	226169-226047	344-384
				63.9	$5e^{-7}$	225631-225338	373-439
PvG25	CAN69431.1	Hypothetical Protein	*Vitis vinifera*	105	$6e^{-62}$	237211-237429	1-72
				163	$6e^{-62}$	237501-237860	93-212
				129	2e-26	237867-238163	1189-1287
PvG26	XP_002268127.1	Peroxidase 16	*Vitis vinifera*	84	e^{-13}	245227-245298	21-70
				109	$8e^{-22}$	243970-243770	70-136
				95.1	$3e^{-17}$	243407-243240	137-192
				204	$9e^{-54}$	242424-241990	182-326
PvG27	XP_004148322.1	Villin-4-like Actin Binding Protein	*Cucumis sativus*	71.6	$5e^{-9}$	267071-266958	19-56
				186	$5e^{-88}$	266468-266031	43-155
				169	$5e^{-88}$	265932-265540	154-258
				87.8	$2e^{-45}$	264396-264235	259-312
				75.9	$2e^{-45}$	264157-264009	313-362
				70.9	$2e^{-45}$	263901-273788	359-396

				93.6	$9e^{-16}$	263037-262876	394-447
				99	$3e^{-27}$	263363-262037	470-553
				66.6	e^{-27}	261634-261530	548-582
				87	e^{-27}	261422-261243	581-640
				84	$8e^{-13}$	260784-260638	634-682
				81.3	$6e^{-12}$	259533-259396	682-727
				43.1	2.3	258576-358522	725-746
				98.6	$3e^{-17}$	257287-256864	747-856
				143	$4e^{-31}$	256245-255862	859-968
PvG28	XP_002319808.1	Predicted Zinc Finer MYM-type protein	*Populus trichocarpa*	29.3	$5e^{-55}$	275370-275071	153-253
				47	$5e^{-55}$	275098-274947	245-298
				113	$5e^{-55}$	274940-274356	323-515
				97.4	$5e^{-55}$	274342-273794	521-570
				85.9	$2e^{-13}$	274029-274580	634-781
PvG29	XP_004242031.1	Protein Disulphide-Isomerase-Like	*Solanum lycopersicum*	61.2	$6e^{-6}$	291729-291547	1-61
				46.6	0.2	286661-286548	53-91
				294	e^{-82}	289486-288659	71-279
				65.9	$2e^{-26}$	288464-288324	272-316
				73.9	$2e^{-23}$	288240-288118	316-356
				66.6	e^{-7}	287957-287835	355-395
				69.7	e^{-8}	286664-286548	395-433
				42	4.9	289453-289250	424-488
PvG30	XP_002284506.1	Uncharacterised Protein	*Vitis vinifera*	104	$4e^{-19}$	301241-300984	1-88
				192	$8e^{47}$	300410-299547	210-450
				81.3	$6e^{-12}$	298565-298359	442-513
				120	$3e_{-24}$	296410-296165	507-588
PvG31	AAN62347.1	CTV.20 RNA Binding Protein	*Citrus trifoliata*	101	$6e^{-18}$	317887-317077	152-439
				111	$7e^{-21}$	316237-315728	672-834

				82	$7e^{-17}$	315292-314646	878-1093
				35.8	$7e^{-17}$	314639-314559	1096-1122
				340	$2e^{-190}$	314297-313530	1152-1407
				167	$9e^{-155}$	315090-314645	1970-2457
				411	$9e^{-155}$	314639-313572	2460-2858
PvG32	CAE01921.2	Hydrolase	*Oryza sativa*	246	$3e^{-67}$	318971- 320023	20-376
PvG33	AAB82639.1	Non-LTR retroelement reverse transcriptase	*Arabidopsis thaliana*	293	$5e^{-95}$	325624-324452	574-965
				85.5	$5e^{-95}$	324395-323682	990-1234
PvG34	CAN80126.1	Hypothetical Protein (Transposase)	*Vitis vinifera*	35	e^{-124}	332170-332295	133-171
				164	e^{-124}	332325-332771	196-344
				300	e^{-124}	332813-333991	360-728
				56.2	$3e^{-4}$	333190-333330	456-502
PvG35	BAF01732.2	NAC Domain Containing Protein 82	*Arabidopsis thaliana*	50.4	0.002	343247-343516	29-121
				43.5	0.38	343247-343453	55-125
PvG36	XP_00352436.1	Aldehyde dehydrogenase family 3 member H1-like	*Glycine max*	62.8	$2e^{-6}$	350969-351067	98-130
				97.8	$7e^{-76}$	351715-351936	131-204
				64.3	$7e^{-76}$	352002-352118	197-235
				70.5	$7e^{-76}$	352216-352332	236-274
				125	$7e^{-76}$	352412-352798	275-366
				74.7	$3e^{-10}$	352893-353078	356-417
				115	$2e^{-23}$	353617-353865	405-487
PvG37	XP_004242040.1	Aspartic proteinase ASP1- like	*Solanum lycopersicum*	70.9	$4e^{-9}$	359616-359736	49-85
				94.7	$9e^{-17}$	360388-360612	88-163
				112	e^{-33}	360842-361087	160-241
				62.4	e^{-33}	361170-362322	241-289
				84.3	$2e^{-13}$	362242-362439	287-352
				43.9	$3e^{-7}$	362890-362970	350-376

				41.2	$3e^{-7}$	363053-363136	377-404
PvG38	XP_002285869.1	Ubiquitin Protein Ligase	*Vitis vinifera*	2109	0	373537-370499	1-1016
				1080	0	369948-367504	1016-1831
PvG39	NP_171677.1	NAC Domain-containing protein 2	*Arabidopsis thaliana*	102	$8e^{-20}$	383458-383297	1-54
				187	$2e^{-48}$	382542-382249	50-147
				119	$4e^{-25}$	381076-380639	145-289
PvG40	XP_003630459.1	Root Specific Metal Transporter	*Medicago truncatula*	72.8	$2e^{-9}$	395388-395269	92-131
				102	e^{-18}	393653-393465	169-231
				48.9	$4e^{-22}$	392861-392778	230-257
				87	$4e^{-22}$	392670-392497	253-310
				70.9	$5e^{-9}$	392359-392111	308-360
				68.9	$3e^{-43}$	391573-391463	385-422
				137	$3e^{-43}$	391394-391053	449-559
PvG41	XP_004250232.1	60S Ribosomal export protein NMD3-like	*Solanum lycopersicum*	26.2	$2e^{-16}$	399357-399304	289-306
				23.5	$2e^{-16}$	399302-399195	308-344
				86.3	$2e^{-16}$	399172-398888	357-453
PvG42	XP_003545652.1	Cyclin-A1-1-like	*Glycine max*	56.6	$3e^{-11}$	407699-407902	142-207
				42	$3e^{-11}$	408016-408120	215-249
				62.8	$8e^{-46}$	408852-408956	251-285
				122	$8e^{-46}$	409052-409366	279-351
				50.1	$8e^{-46}$	408962-408956	350-374
				76.3	e^{-10}	409799-409975	373-438
				64.7	$4e^{-7}$	410103-410228	444-485
PvG43	XP_003634405.1	Amino Acid Permease 2	*Vitis vinifera*	43.5	1.5	420367-420456	13-39
				137	$3e^{-30}$	420833-421069	39-117
				63.9	$2e^{-58}$	421735-421830	117-148
				130	$2e^{-58}$	421934-422146	149-219
				83.6	$2e^{-58}$	422251-422391	220-266

PvG44	ABD32582.1	Integrase catalytic region Zinc Finger, CCHC-type aspartic peptidase	*Medicago truncatula*	272	0	430798-431697	659-956
				47	0.2	431699-431782	957-984
				380	0	431754-432947	980-1387
				195	0	432998-433384	1393-1521
				245	0	433378-433959	1517-1710
PvG45	XP_002284607.2	NAD Kinase 2	*Vitis vinifera*	595	$4e^{-180}$	441784-440051	84-742
PvG46	Q9ATE5	MADS-box protein FBP24	*Petunia x hybrida*	110	$2e^{-22}$	451899-452087	2-64
				77	e^{-11}	453210-454569	65-146
				45.1	0.26	456474-456665	197-259
PvG47	XP_002278437.2	Uncharacterised WW domain containing protein	*Vitis vinifera*	43.1	2.2	465350-365358	118-148
				72.4	$2e^{-9}$	462094-462934	236-292
				52	0.004	461297-461076	288-373
				83.2	$7e^{-13}$	460191-459853	405-464
				69.3	$2e^{-8}$	458886-458770	465-503
PvG48	AFP55536.1	Retrotransposon Polyprotein	*Rosa rugosa*	96.7	e^{-16}	476072-475305	508-770
				49.7	0.028	475873-475751	577-617
				59.7	$3e^{-26}$	474798-474322	969-1130
				58.2	$3e^{-26}$	474286-474119	1170-1225
				51.6	$3e^{-26}$	474071-473919	1242-1292
PvG49	ABD78321.1	MADS- box gene: Glo Protein (*PvGLO)*	*Primula vulgaris*	132	$2e^{-30}$	481859-482047	1-63
				51.2	0.001	482536-482601	64-85
				90.9	$2e^{-16}$	483151-483432	85-140
				42.7	0.97	485382-485438	150-168
				85.5	e^{-14}	486463-486579	169-207
PvG50	XP_002520299.1	UDP-n-acetylglucosamine pyrophosphorylase	*Ricinus communis*	47.4	0.11	493505-493591	43-71
				70.5	$8e^{-28}$	494937-495059	70-110
				84	$8e^{-28}$	495152-495307	106-157
				57.8	$7e^{-5}$	496081-496182	157-190

				79.7	e^{-21}	496814-496972	169-232
				54.7	e^{-24}	497053-497304	232-279
				106	$5e^{-20}$	497850-498110	279-338
				99	e^{-17}	499047-499430	337-405
				75.1	$3e^{-10}$	499678-499974	405-463
				57	e^{-4}	500408-500494	460-488
				127	e^{-26}	500896-501177	473-568
				87.4	$6e^{-14}$	501728-501895	567-622
PvG51	XP_002520262.1	2-oxoisovalerate dehydrogenase	*Ricinus communis*	117	$3e^{-24}$	505633-506034	1-93
				165	$5e^{-40}$	506693-507034	93-179
				72.4	8e-10	507352-507471	178-217
				63.5	5e-7	507779-507919	218-264
				120	$4e^{-250}$	508340-508573	264-341
				68.6	e^{-8}	509110-509262	329-379

Table 5.1: Genes identified within the assembled *P. vulgaris* sequence. A proposed identity is shown for each gene based on a match to a subject from another species. The score and E-value for each match is also shown as are details of the regions within the query sequence and subject sequences that match.

5.2.2 Annotation of *Primula vulgaris* genes

Following the identification of the nature of the genes contained within the assembled *Primula vulgaris* contig, the 51 genes were analysed further to predict their unique amino acid sequences and, subsequently, their nucleotide sequences. The same procedure was followed for all 51 genes identified (as described in 5.2.1.) though *PvG46*, the MADS box gene *FBP24* from *Petunia x Hybrida* is shown in detail as an example. The choice of *PvG46* as an example is due to its function as a MADS Box protein, which, upon first identification, initially made it a candidate for *sepaloid* (discussed further 5.3). As such, this gene was of particular interest during the annotation process.

5.2.2.i Identification of *Primula vulgaris* open reading frames

Following identification of *PvG46* within the assembled *Primula vulgaris* sequence, the accession number of the identified subject gene *Petunia x hybrida FBP24* (as shown in Table 5.1) was used to retrieve he full amino acid sequence of the subject protein from the NCBI database. This sequence was then annotated to highlight the sequences identified in the BLASTX search, described above, as shown in Figure 5.1.

MIIMGRGKIEVKRIENKTSRQVTFSKRRAGLLKKTHELSVLCDAQI
GLIIFSSKGKLFEYCSQPHSMSQIISRYLQTTGASLPVEDNRVQLY
DEVAKMRRDTLNLQLSLQRYKGDDLSLAQYEELNELEKQLEHALNK
IRARKLELMQQQMENLKKTEKMLEKENHDMYQWLMNNQMYKQESAA
MDHEDHHHHHEHQQAITELNLLGEQPLLSHFTFFGDQEQPSTSTVN
HFASISLTSPPANSISPYRLQPSHPNLQDSHVHGPSYD

Figure 5.1: The amino acid sequence of the *Petunia x hybrida* gene *FBP24*. The four regions identified through the NCBI BLASTX search with *Primula vulgaris* genomic sequence are highlighted.

In Figure 5.1, green highlighting represents the first subject region described in Table 5.1, followed by yellow, blue and grey. The same order of colours was then used through the annotation of the gene to signify proposed exons.

The ExPASy Translate tool was used to translate the region of the *P. vulgaris* sequence known to contain *PvG46*, as well as 1kb of sequence to either side of the predicted gene sequence. All open reading frames were analysed and the same amino acid sequences highlighted in Figure 5.1 were identified within this translated sequence.

5.2.2.ii Annotation of *Primula vulgaris* gene amino acid sequences

Using the *Petunia* sequence shown in Figure 5.1 as a guide, the same sequences were identified within the different frames of the translated *Primula* sequence and highlighted in corresponding colours. These sequences were subsequently considered to be the translated exons of *PvG46* and were expanded on.

Although the highlighted regions of sequence in Figure 5.1 provided the core of the *Primula* gene exons, these needed to be expanded upon to obtain their predicted full exon sequence. In order to do this, and identify intron/exon splice junctions, the original *P. vulgaris* nucleotide sequence was used in conjunction with its translated form. All intron/exon boundaries were identified using the GT-AG rule and care was taken to ensure that the boundaries accounted for any changes in reading frames between exons.

The codons responsible for the highlighted amino acid sequences were identified, and these preliminary exons were extended by incorporating nucleotides to both ends of the exon until either a GT (marking the start of an intron) or an AG (marking the end of the intron) was reached. In some instances, nucleotides were removed from

the preliminary exons sequence in order to achieve this. In the case of the first exon, nucleotides were either incorporated or removed to ensure that an ATG Methionine codon was reached. Similarly, the final exon was extending until a stop codon was reached.

Following the identification of intron/exon boundaries, the exons were combined to form the predicted amino acid sequence of *PvG46*, shown in Figure 5.2.

***PvG46* – Amino Acid Sequence**

MGRRKTELKRIENTTSRQVTFSKRRSGLMKKTHELSVLCDAQIGLIVFSNKGKLYEYSS
HPMMGEIIEKYLTATGDCIPVNDNRVISLKLN**L*T*LSN*LE*AISFLV*ALVPKLT
K*MQEQMCSELLKLKKETDSLQLSLQCYKGQDLAYVQYDDLAQLEHQLECSLNKVRARK
VRIPYYWLDFSDKMLEKENLEMFHWVENQHQQVMTELKLVGDQQQQMFMDHFRFFGEQQ
QLVQPNANTHTGLLYQSLQLNNSFRLQPAQPNLQDPSSSTLALLQSYGIYDTYVYDAFQ
GIVWLHLSHLAF

Figure 5.2: Predicted amino acid sequence of *PvG46.* * represents a stop codon.

5.2.2.iii Annotation of *Primula vulgaris* gene nucleotide sequences

With the annotation of the amino acid sequence of *PvG46*, the nucleotide sequence

***PvG46* – Coding Sequence**

ATGGGTAGAAGAAAGACAGAGTTGAAGAGGATAGAGAACACCACAAGCAGGCAAGTGACTTTCTC
AAAAAGAAGAAGTGGCCTAATGAAAAAAACTCACGAGCTTTCAGTTCTTTGCGATGCTCAAATCG
GCCTCATTGTTTTCTCCAACAAAGGGAAGCTCTACGAGTATTCGAGTCATCCTATGAGCATGGGG
GAAATCATTGAGAAGTATCTGACTGCTACAGGAGATTGTATACCAGTAAATGACAATCGGGTAAT
TTCTCTCAAGTTAAACTAATAATTGTGAACATAGTTGAGTAATTAACTTGAATAAGCAATATCTT
TTTTGGTTTAGGCTCTAGTTCCCAAACTAACCAAATAGATGCAGGAGCAGATGTGCAGTGAGTTG
CTGAAATTAAAGAAAGAAACTGATAGTCTTCAACTAAGCCTGCAATGCTACAAAGGCCAAGATTT
GGCGTATGTCCAATATGACGATCTCGCTCAGCTCGAACATCAACTAGAGTGCTCGCTTAACAAGG
TCCGTGCAAGAAAGGTACGTATTCCATACTATTGGTTAGATTTTTCAGACAAAATGTTGGAAAAG
GAAAATCTGGAGATGTTTCACTGGGTAATTGAGAACCAGCACCAGCAGGTTATGACTGAGTTGAA
GCTAGTTGGAGATCAGCAACAACAAATGTTTATGGACCATTTCAGGTTCTTCGGCGAACAACAAC
AACTAGTGCAGCCCAATGCTAATACTCACACTGGGTTACTATATCAGTCTCTCCAGCTCAACAAC
AGTTTCCGCCTTCAGCCCGCTCAGCCTAACCTCCAAGACCCCAGTTCCTCCACCCTTGCCCTCCT
CCAATCGTATGGTATATATGATACATACGTATACGATGCATTTCAAGGGATTGTTTGGTTGCATC
TTTCCCACTTAGCATTT

Figure 5.3: Predicted coding nucleotide sequence of *PvG46*.

for each exon could also be identified. These nucleotide sequences were combined to construct the predicted coding nucleotide sequence of *PvG46*, shown in Figure 5.3. Annotation of the predicted coding sequence for *PvG46* meant the exon sequences could also be identified within the assembled contig of *Primula* genomic sequence. This also served to identify the sequences of the introns between them. Figure 5.4 shows the predicted genomic DNA sequence of *PvG46*, as well as the 500bp found at both the 5' and 3' ends of the identified sequence.

***PvG46* – Predicted Genomic DNA Sequence**

AAACTTGTTTCCTTTTTCACTACTGGGTAGATCAAAGAGATCAGCAATGGTTAGAGTGTAACAAAACT
GAAGAGGGTTGAGGTTAAAACTTTTATTAATTAAGTTCTATCCAAAACTTAACTTTTCATCACAATAT
TTTCAAATAAAAGTTTGTTTGTTTTTGCCTTTGAGAGGGTAAATTACGTTATCCTTTTTTTCCTTGTT
TATATATGTTTTTCATCAGGTAAATCAAAGAGACAATCTTGACTAGAGGAATAACTAGTAAATATGAT
TGAGAACATGATCATGAACACATGACTACTTATCAAATTAATTTAGCTAAAAAAAAAAATAATCGTTTT
CTATAACAACAGTACTTTAAAATGCATTTGCTTATGAGTTTTGTAGGGTTTTTGAATTTTTTTTTCCT
AAGTATTTATTTCTTTCTAGAAAATTGTCTGTGGTCTTTTATTTTATTTTTCTTTAGCTATTAAATTA
AATGAGTTTTTTTCCTCTTTAGTC**ATGGGTAGAAGAAAGACAGAGTTGAAGAGGATAGAGAACACCAC**
AAGCAGGCAAGTGACTTTCTCAAAAAGAAGAAGTGGCCTAATGAAAAAAACTCACGAGCTTTCAGTTC
TTTGCGATGCTCAAATCGGCCTCATTGTTTTCTCCAACAAAGGGAAGCTCTACGAGTATTCGAGTCAT
CCTATGAGGTCTTTTTTTATTTCCCTTTTGTTTTATATTTTTCTTTTCTGGCATTCTTATAAGTTTCT
TTTTTAATTCCCAAATTCACTGCTTTGTATTTTGTTACTAATCTTTTGTTAGTTTTAGCCCCCCAAAA
ATATTGCTCTTTCTTATATTAGTACGTATCACGATTCTTAATTTTTCTCCTTAAGTTCTACTTATAAG
ATTGTATAATCTTCTTTGAAGTTTGAAACTCAAGTCCTTTGCTTGCACTTTCTTTTGTGTAATTCACT
ATTAGACGTACTTTTGATACTTAATCATCAAAATGTCACACATCAATGTTTAAACTTTCTTAATGTTA
CTCTTAATTTTTATCTTGATTCTTAATTTTTCTCCTTTAGTTCTACTTATAAGATTGTATAATCTTCT
TTGAAGTTTGAAACTCAAGTTCTTTGCTTGCACTTTCTTCTATCATGCGTGAAATGGATGTCAATGTC
ATTTAACCAAGTAATTAATAACGGCACTCATATATGAATTTTTTTTCCATCTCTTTGAGGTTTTGTTT
TCCTAAATAATATTCATTTTCTTGGGCTCGTTTAATTTTTATATAGAATCAAAGTAAATATGGCTTTT
ACAATACAATACTTTTCTTTCGCAATGTACCATTTTCTGTTTATTTTGGTAAATTTCACATTTAGATA
TTTTCCAATACGATCATGGGTGTCAAAATATATAAATTTATCAATTTTAGTTATTTCCATCCGTCACT
CTCTCACAAACTCAAACCATTAGATACTTATTTGACTAACTTGAGTGATTTGACAAATATCTGACTGA
TCACTCATCACATGCTTAGTAATTATTGACAGTAATTACTTGACCAAATTTTCTGTCAATTTGAAAAT
ATTTTTTAAGAAAATTAACATGGTGCCTTTTCATGTTCTTCACTAGTAAGTGTAATAATAAGAATTTC
CAAATGATCCAGAATAAAGTAATTAATACTCTAAATATATGAAACCTTCACGTGTCACACTGGTTTCT
TAAAATAAGACCGTCACATATATGAAATTATGAACCAAAGTCTTGCAAACGTCTTGAAATATTTGACA
TTTATGTAATTGAATTTATATATGTCTTTTGTATTCCTACAG**CATGGGGGAAATCATTGAGAAGTATC**
TGACTGCTACAGGAGATTGTATACCAGTAAATGACAATCGGGTAATTTCTCTCAAGTTAAACTAATAA
TTGTGAACATAGTTGAGTAATTAACTTGAATAAGCAATATCTTTTTTGGTTTAGGCTCTAGTTCCCAA
ACTAACCAAATAGATGCAGGAGCAGATGTGCAGTGAGTTGCTGAAATTAAAGAAAGAAACTGATAGTC
TTCAACTAAGCCTGCAATGCTACAAAGGCCAAGATTTGGCGTATGTCCAATATGACGATCTCGCTCAG
CTCGAACATCAACTAGAGTGCTCGCTTAACAAGGTCCGTGCAAGAAAGGTACGTATTCCATACTATTG
GTTAGATTTTTCAGTTTATAACCATTTTCGATAACGATTTTATGTCTTTCAACGTGTGTTTTTCCTAT
AATTGACAAGGCACCTCCAAACTTGATCTTAAAAAAAAGGCACCTCCAAACTTTTAAAAGGTTTAGTT
ACATCTGTAAGATACTTAAACTTTGTTTTCTTAAATTGATAATTTTGAAAAATCAAAACCTTTAAATT
TCACATTATGTATATGACTTGGCTAGCTAGGTTTTGTAAAATAATTCTAGGTCCCATTTCTCACAAAA
AGGTGAAAATGGAAAGTGTCGTGTTGTACATTATATTTAGGGCTAGACCTAGTGACAACTAAACGAGC
TGTCAGTTAAGTCGTCGATCCCCGAATATAAAGAAAAGAAAATAATGCAAAACAACGTATTTTTCCCC
CTGAAGCAATGTATGGAATTAGAAACAATTTTTTCTGATGGTTTATTTTGTATTGTGTGAAAGTATTT

TGTGACCTTGTGAGAGACTTTATAATTTTTCTATGAAATTTATATTTTGGTATAGTATGAATTTTTCA
GACAAAGTTCTAAAAAGTCCAAAATATTGTGCAGAGTCGACCCTAGGTCACCATATACATTAAGTATC
GAAGTACCTGAGGTTTAACATTTTGTCGATTTAGTCTCAATTGTTTCATTTTTTAATCAATTGCACCC
ATTTCATTTAGTCATCAGTTAGGTCGTTTTATTATTTTTGGACCATTTCGCCTTTCAAAGGTTTTGTT
AAACTATGCTAACAATTGAAATAATTGAATTATCCTATGCTACATGTGAAATATTTAGAAAAAATCTT
TTCATCACCAAATTTTCAAACCCAAAAACCTAACACGTAATCTTTGTTGTAATTTTGAAAACTAATTT
TCATTTAATATATAATTGTTCCACGTAAACTGTCACATCAGCATGTAAGAGTTTGGGGTAGCTATAGC
AATACTAAAATATTTAATTTTACATCAATTGTTATCCAATATTTCATTTATACGAATAATATCATTTA
TAATCTAGTTATTCACCTACCAATAAAGATTCAGAATCATAAATTTATTTATATTATGTACTATATGC
ATAGGACAGATGCATACATATTCAACACTGTTTCACTAAACATTTACGTGAATATGAAAGGAGACTTT
TAAATTGATGTCTTGATAGAAGAAAAAATAGAAGATCATGGAAAGAAGACTTTAATTAATGAGTAATA
ATTTATCGACAAAAAATAATAATTATTATTTTTGTAATCTCGACAAAAAATAACTATATGGGACTACT
TAAGTTGATAAAAGGGTAAACCACGGGCTCGGGTTGTTTTTTTTATAGTTGCCCTTGTATTATTAACA
TAACCCCTAGACATTGTAAACAAACTTTATATGAAGGGGTTCTTCTTCGATATATTTATGCCCTTTTT
CTAATAGTTTTTGTTTGTCTGGAATTCTGCAGAATCAGCTCTTGCAGCAACAGTTGGACAATCTACAA
AAAAAGGTAATTTAACAATAAAACTTTCATTCAGCAAGTTTGTAACTACAGTTTCAGCCTGAAAACAA
CTTCGCCGTCCTTTGACAACTCGACCATCGAGTGTTGCTCGTTGATAACTTGTCACGACAAATTAGCC
ATATATCTAACCATGTCCACACAGAGCAATAGTTTTAACACGATATACATGTCGCAAAAAGTAAGTCT
TTTGTTGGAATTCACCTCAGTAAATGATACTTATGTGTATACTCTTGAACTTTTTCATGGTAAACGTA
GCATATACACACTCCATCTGTACAACTTAAAGATAAACACATCTTAGTTTAAACATTTCACATAAATT
TGTAAATGTACCTAGCTTGATTTTAATTGTAAATGTTCTTCTTTTTCTTGTACCAG**GACAAAATGTTG**
GAAAAGGAAAATCTGGAGATGTTTCACTGGGTAAGTGAAGTTTTATTTAATTATTTTCCAAATTCCTG
CATAAATGTGATACTGTTGACGCGCTAAGTACCATGTTATATGATAAAACTGACAAACTAAATGGTTT
ACATAATATCTTGATTATTAAAAGGTGAATTTGATTTTGTGCTTATAAAGTAATCACTTGAGGAAACT
AACTAGAGGTTTGAGCAACATGGAAAAAAAAACACGTTATCAATTTTTTTTGCCTAAAAAAGCTGTAC
AATTATGTTGGGATTATATACACTTAAAGAATATATAGTACGCAATGTCGCATACAGTTTTGCTGCCA
AAACAATTTAAATATTTGTAAATCAAATGTGATAGACTTGTTTATGATCAACATTTTGGTTGTTGCTA
CCCGAGAACTCAGCGAGATATATCTGTCACTGAAAGGTCAACTAGATCAATCCGAGTATGTAAGGAAT
AATGTTGGATATCAATCGATCATTACTCCATGCTTATCTTAGGATGGGTAAGAAAATACGGAGTACGA
TTCCATTGCTTTAGAAGATAGGCACTCTGATTATCTTGTAAGAAACTTACTTTTAGTATGACATAATT
GGCATGAATTGAATGTAAGAACTAATTTGGAACATTTTATTCTTTTTCAATACAAGCCAAGTTTTATG
TTCAAACAATGATTTTATTAGCAGGGTTGGTTTATAAGTCAAAGTCATGTATGCAGCATCTATGTTCT
ACATTTTTCAGGTCATAATAAACAAAATCAAAACATAGTTTTAATCTGGTTAACCAATTGCATCGCAG
CTCACAAGTAAACTGAACACTTAAACATGACAGCCGCTGTTACAAAACATCCCCAAATCTTGGGATAC
CTAAATATTCCTTTTTTTAAATATCTTTCTTCTTGCGTTTGTAGCTAATTGTATATATACATTATTTC
GGTATAGTTGGCAGGTAACCAAG**TTGAGAACCAGCACCAGCAGGTTATGACTGAGTTGAAGCTAGTTG**
GAGATCAGCAACAACAAATGTTTATGGACCATTTCAGGTTCTTCGGCGAACAACAACAACTAGTGCAG
CCCAATGCTAATACTCACACTGGGTTACTATATCAGTCTCTCCAGCTCAACAACAGTTTCCGCCTTCA
GCCCGCTCAGCCTAACCTCCAAGACCCCAGTTCCTCCACCCTTGCCCTCCTCCAATCGTATGGTATAT
ATGATACATACGTATACGATGCATTTCAAGGGATTGTTTGGTTGCATCTTTCCCACTTAGCATTTTAA
AGTATAAATGCATACCTACGAATACGAAGCATTACGGTATAAATACTCACATCCGAATACGAATACGA
TTTGGTACATTTTTTAGTTGAAAAGGTCGCGACTTTTAAGACGGATTAACCTTTTTTGCAGACAAGGC
CATCTATAAAAAAGTTACAGAGGGTCGAGATTATATGCCCCAATGATATTAGATTGGTTATGATAAGC
TATTCTTAATATTGTTTGGATATTCCCTTCACTAATTAGTTGATGATTTGCAGATCAGTGATTATTCG
CAAGGAACATAGCGATGAAGCTTGCTGGACATTGTTAAATACTGGTGATACTGGAGAGAAATTACTAG
TTTTTTAGGTTTAAAAGTTCTAAAAAGAAAAAGCATATCATATGCAATACTTTCTTTATATCCATGCT
TGGTTTGCCTAGAGATTTGATGGTATAACTTTTATTTGGTGAAGTGTTGCCTAACTGCTTACTACTGC
CTGAAATATTGATGTTGCTTGA

Figure 5.4: Predicted genomic DNA sequence of *PvG46*. Exons are shown in bold. Figure includes 500bp beyond both ends of identified gene sequence.

As described in 5.2.2, the same procedure was followed for each of the 51 genes identified and described in Table 5.1. The predicted genomic sequences for all 51

genes, including 500bp beyond both 5' and 3' ends, can be seen in Appendix C. A summary of these results is shown in Table 5.2.

Gene	**Orientation**	**Exons**		**Introns**		**Coding Sequence Length (bp)**	**Genomic Sequence Length (bp)**
		Exon #	Size (bp)	Intron #	Size (bp)		
PvG1	+/+	1 2	152 99	1	2962	251	3213
PvG2	+/+	1	264			264	264
PvG3	+/-	1 2	1033 293	1	2508	1326	3834
PvG4	+/-	1 2 3	413 3791 1020	1 2	23 11	5224	5258
PvG5	+/+	1 2 3 4 5	195 104 371 308 249	1 2 3 4	5420 209 578 383	1227	8317
PvG6	+/-	1 2 3 4	133 293 352 629	1 2 3	941 1887 1382	1407	5617
PvG7	+/-	1	888			888	888
PvG8	+/+	1 2 3 4 5 6 7	86 228 221 158 451 419 564	1 2 3 4 5 6	1231 617 734 265 574 172	2127	6221
PvG9	+/+	1 2	876 615	1	1186	1491	2677
PvG10	+/+	1 2	885 609	1	441	1494	1935
PvG11	+/+	1	612			612	612
PvG12	+/+	1	270			270	270
PvG13	+/-	1 2 3 4 5 6 7	249 112 431 219 276 279 102	1 2 3 4 5 6	1491 128 88 560 406 89	1668	4430
PvG14	+/+	1 2 3	175 578 399	1 2	362 26	1152	2040
PvG15	+/+	1	693			693	693

PvG16	+/+	1 2 3 4 5 6 7 8 9 10 11	166 281 85 248 405 230 118 132 138 207 165	1 2 3 4 5 6 7 8 9 10	494 428 235 357 368 277 146 85 118 360	2175	5543
PvG17	+/+	1 2	310 350	1	2166	660	2826
PvG18	+/+	1 2 3 4 5 6 7 8 9	81 237 105 276 145 190 68 295 168	1 2 3 4 5 6 7 8	1986 100 470 461 332 133 161 371	1565	6079
PvG19	+/-	1	306			306	306
PvG20	+/-	1 2 3 4 5 6 7 8 9 10	178 74 176 84 70 256 79 79 68 165	1 2 3 4 5 6 7 8 9	112 519 76 116 82 109 112 109 242	1229	2706
PvG21	+/+	1 2	455 646	1	939	1101	2040
PvG22	+/+	1 2 3	381 50 55	1 2	473 82	486	1041
PvG23	+/-	1 2	1357 761	1	495	2118	2613
PvG24	+/-	1 2 3 4 5 6 7 8 9 10	99 285 87 90 81 69 78 126 100 104	1 2 3 4 5 6 7 8 9 10	563 107 122 74 94 77 427 429 76 182	1503	4105

		11 12	106 278	11	451		
PvG25	+/+	1 2	213 663	1	80	876	956
PvG26	+/-	1 2 3 4	228 186 171 372	1 2 3	1318 374 875	957	3524
PvG27	+/-	1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17	56 112 408 389 163 142 101 156 69 288 129 125 157 126 66 318 387	1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16	853 516 104 4081 83 118 759 369 77 414 125 485 1107 828 1323 621	3192	12117
PvG28	+/-	1 2	266 1514	1	17	1780	1797
PvG29	+/-	1 2 3 4 5 6 7	166 824 115 120 118 104 186	1 2 3 4 5 6	2753 221 86 166 1182 1826	1633	7201
PvG30	+/-	1 2 3 4	2196 176 224 751	1 2 3	1011 1969 778	3347	6605
PvG31	+/-	1 2 3 4 5 6	885 553 544 782 719 410	1 2 3 4 5	131 159 363 314 743	3893	5583
PvG32	+/+	1	1056			1056	1056
PvG33	+/-	1 2	1087 702	1	97	1789	1886
PvG34	+/+	1 2	209 1693	1	80	1902	1982

PvG35	+/+	1	329			329	329
PvG36	+/+	1 2 3 4 5 6 7 8	207 69 238 107 105 375 150 228	1 2 3 4 5 6 7	2289 853 92 94 79 127 577	1479	5590
PvG37	+/+	1 2 3 4 5 6 7	117 224 233 139 195 74 92	1 2 3 4 5 6	655 242 85 934 459 81	974	3530
PvG38	+/-	1 2 3 4	3039 2545 455 318	1 2 3	553 617 1580	6357	9107
PvG39	+/-	1 2 3	160 278 432	1 2	769 1181	870	2820
PvG40	+/-	1 2 3 4 5 6 7 8 9 10	144 82 105 110 182 70 189 312 99 339	1 2 3 4 5 6 7 8 9	565 119 469 1035 609 122 131 465 83	1632	5230
PvG41	+/-	1	267			267	267
PvG42	+/+	1 2 3 4 5 6 7 8	203 115 93 306 60 195 135 60	1 2 3 4 5 6 7	104 728 116 106 251 112 390	1167	2974
PvG43	+/+	1 2 3 4 5 6	124 234 94 214 140 651	1 2 3 4 5	379 668 104 104 176	1457	2888
PvG44	+/+	1 2	679 887	1 2	1041 26	2583	4872

		3 4	58 959	3	1222		
PvG45	+/-	1 2 3 4 5 6	1704 344 234 75 102 201	1 2 3 4 5	552 496 528 848 771	2660	5825
PvG46	+/+	1 2 3 4	188 379 46 314	1 2 3	1122 1879 941	927	4869
PvG47	+/-	1 2 3 4 5 6 7	79 107 57 171 114 337 150	1 2 3 4 5 6	1118 326 1731 1083 537 966	1015	6776
PvG48	+/-	1 2 3	761 481 371	1 2	521 38	1613	2172
PvG49	+/+	1 2 3 4 5	188 67 303 57 117	1 2 3 4	488 552 1925 1024	732	4721
PvG50	+/+	1 2 3 4 5 6 7 8 9 10 11 12	270 117 141 100 128 245 260 379 286 81 240 165	1 2 3 4 5 6 7 8 9 10 11	1351 107 776 664 83 548 942 250 445 443 556	2412	8577
PvG51	+/+	1 2 3 4 5 6	402 339 112 140 186 165	1 2 3 4 5	661 323 307 423 575	1344	3633

Table 5.2: Summary of the structures of *PvG1-51*

Following annotation of each of the 51 genes described in Table 5.1, a Northern blot to determine the expression profiles of *PvG1-51* was planned. Whilst time constraints prevented the completion of this planned investigation, primers were designed to amplify the 3' UTR region of each gene from Pin genomic DNA by PCR using Go-Taq polymerase. Standard PCR protocol, as described in 2.2.2, was followed. Primers can be seen in Appendix A and the results are shown in Figure 5.5.

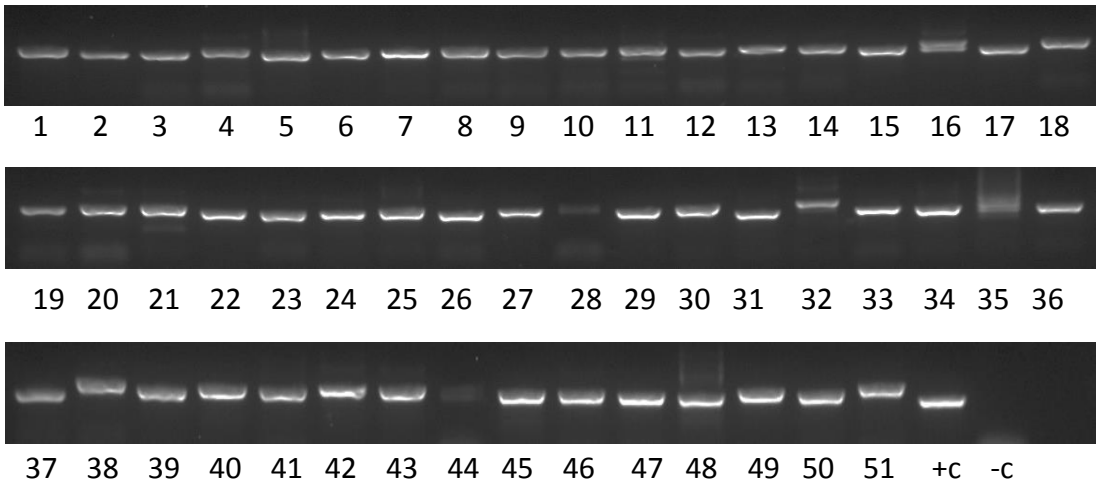


Figure 5.5: PCR amplification of *PvG1-51* 3' UTRs. Results of PCR showing genomic DNA amplified from 3' ends of 51 genes identified from the assembled *Primula* sequence. A positive control (+c) and a negative control (-c) were also included.

5.3 Discussion

The initial BLASTX search described in 5.2.1 yielded important and interesting results. The first of these was the identification of both *PvSLL1* (*PvG2*) and *PvGLO protein* (*PvG49*), within the assembled sequence, the presence of which was expected due to the way that the sequence was originally constructed. However, the

presence of these two genes is important as they demonstrate very different patterns of recombination. Pv*SLL1*, characterised as a tightly linked marker of the *S*-locus (Li *et al.*, 2007) never recombines with the *S* locus where-as recombination does occur between the *S* locus and *PvGLO*. As such, the presence of these two genes within the assembled contig demonstrates the sequence must span the region within which the system that limits recombination in the *S* locus breaks down. As stated above, the exact nature of this system remains unknown though, evidence suggests that the *S* locus is situated near to the centromere of its chromosome, where recombination is typically limited (Li *et al.*, submitted)

The nature of the other genes identified within the region is also interesting. The majority of searches returned successful hits to genes of known function from other plant species. Among these, 10 genes were identified that did not have a characterised function. 3 of these, *PvG15*, *PvG25* and *PvG34*, were identified as Hypothetical Proteins from *Vitis vinifera*. Due to the largely uncharacterised nature of the *Vitis* genome within the NCBI database, a number of genes such as these exist and, whilst the gene has been predicted, it remains to be proved that *PvG15*, *PvG25* and *PvG34* are truly functional genes. However, since they cannot be dismissed with any certainty, they will continue to be included among the other 48 *Primula* genes identified. The remaining 7 uncharacterised genes were identified from a variety species. Although some (*PvG11*, *PvG17*, *PvG19*, *PvG22* and *PvG30*) gave no indication as to their function, *PvG24* and *PvG47*, had suggested functions due to similarities with chaperonin proteins (*PvG24*) or the presence of a Tryptophan containing domain (*PvG47*). As such, despite an uncharacterised function for 5 of these 7 genes, it can be assumed that all 7 are true, functional genes in *Primula*,

whose function could be determined in the future, and will also continue to be included.

Table 5.1 also shows a number of other interesting genes identified by BLASTX searches of *Primula* genomic DNA. Two such examples are two genes (*PvG9* and *PvG10)* identified within *Primula* that display homology to the same Cytochrome P450 gene from *Populus trichocarpa*. In addition to this shared subject match, the two genes were identified in close proximity to each other within the *Primula* contig, suggesting possible gene duplication. *PvG23*, a *Pentatricopeptide-repeat containing* gene, also showed an interesting pattern when it was identified within the *Primula* coting, with more than one region within the sequence mapping to the same parts of the gene. Again, this may suggest possible gene duplication within *Primula* but may also be a result of a repetitive nucleotide sequence, resulting in numerous matches between query and subject.

The gene identified as *PvG46* also attracted attention due to its identity as a MADS-box gene, specifically a homologue of the *Petunia x hybrid* gene *Floral Binding Protein 24* (*FBP24*). As stated in 1.8, the region between *PvSLL1* and *PvGLO* is of interest as it is thought to be the area in which *sepaloid* (discussed in 1.6.2) is located. As such, the identification of a MADS-box gene within this region was of particular importance in the search for the *sepaloid* gene. Furthermore, the initial identification of *PvG46* as a homologue of *FBP24* provided further evidence in its favour as *FBP24* had been demonstrated to be a B(sister) MADS-box gene, closely related to the B function genes that are instrumental in the development of the second and third whorls of the flower in *Petunia* (de Folter *et al*., 2006; Coen and Meyerowitz, 1991). However, further investigation into the role of *FBP24* in *Petunia*, revealed that it was more specifically involved in ovule development,

making it a less likely candidate for *sepaloid* (de Folter *et al*., 2006). In addition to this, sequencing of the *FBP24* cDNA sequence extracted from *sepaloid* floral tissue showed no difference to that extracted from wild type individuals. An alignment of these two sequences can be seen in Figure 5.6.

Following the rejection of *PvG46* as a candidate for *sepaloid*, *PvG49*, a second MADS-box gene identified within this region remained as the only candidate. As identified in Table 5.1 though, *PvG49* was identified as *PvGLO*, a gene previously rejected as a candidate for *sepaloid* following the discovery of a Thrum specific allele (see 1.7.3) and since attributed to the *Hose-in-Hose* mutation (Li *et al*., 2008, 2010). As such, this gene was not investigated further at this point and it was assumed that *sepaloid* must be located near to but outside of the region being examined as no other credible candidates were found. However, despite its rejection of *PvGLO* as a candidate for *sepaloid*, the generation of a *sepaloid* genome, sequenced subsequent to this investigation and unavailable prior to completion of this work, has allowed for comparisons of this gene between the *sepaloid* and wild type genomes. Preliminary analysis of this genome sequence has suggested that a polymorphism, leading to the deletion of an intron of *PvGLO* may exist within the *sepaloid* genome but, whilst this provides further evidence of a link between *PvGLO* and the *sepaloid* mutation, the existence of an apparent Thrum allele of *PvGLO* remains to be explained.

```
Pin                                                                   ATG
Sep                                                                   ATG
                                                                      ***

Pin     AAAAAAACTCACGAGCTTTCAGTTCTTTGCGATGCTCAAATCGGCCTCATTGTTTTCTCC
Sep     AAAAAAACTCACGAGCTTTCAGTTCTTTGCGATGCTCAAATCGGCCTCATTGTTTTCTCC
        ************************************************************

Pin     AACAAAGGGAAGCTCTACGAGTATTCGAGTCACCCAATGAGCATGGGGGAAATCATTGAG
Sep     AACAAAGGGAAGCTCTACGAGTATTCGAGTCACCCAATGAGCATGGGGGAAATCATTGAG
        ************************************************************

Pin     AAGTATCTGACTGCTACAGGAGATTGTATACCAGTAAATGACAATCGGGAGCAGATGTGC
Sep     AAGTATCTGACTGCTACAGGAGATTGTATACCAGTAAATGACAATCGGGAGCAGATGTGC
        ************************************************************

Pin     AGTGAGTTGCTGAAATTAAAGAAAGAAACTGATAGTCTTCAACTAAGCCTGCAATGCTAC
Sep     AGTGAGTTGCTGAAATTAAAGAAAGAAACTGATAGTCTTCAACTAAGCCTGCAATGCTAC
        ************************************************************

Pin     AAAGGCCAAGATTTGGCGTATGTCCAATATGACGATCTCGCTCAGCTCGAACATCAACTA
Sep     AAAGGCCAAGATTTGGCGTATGTCCAATATGACGATCTCGCTCAGCTCGAACATCAACTA
        ************************************************************

Pin     GAGTGCTCGCTTAACAAGGTCCGTGCAAGAAAGAATCAGCTCTTGCAGCAACAGTTGGAC
Sep     GAGTGCTCGCTTAACAAGGTCCGTGCAAGAAAGAATCAGCTCTTGCAGCAACAGTTGGAC
        ************************************************************

Pin     AATCTACAAGAAAAGGACAAAATGTTGGAAAAGGAAAATCTGGAGATGTTTCACTGGTTG
Sep     AATCTACAAGAAAAGGACAAAATGTTGGAAAAGGAAAATCTGGAGATGTTTCACTGGTTG
        ************************************************************

Pin     GCAGGTAACCAAATTGAGAACCAGCACCATCAGGTTATGACTGAGTTGAATCTAGTTGGA
Sep     GCAGGTAACCAAATTGAGAACCAGCACCATCAGGTTATGACTGAGTTGAATCTAGTTGGA
        ************************************************************

Pin     GATCAGCAACAGCAAATGTTTATGGACCATTTCAGGTTCTTCGGCGAACAACAACAACTA
Sep     GATCAGCAACAGCAAATGTTTATGGACCATTTCAGGTTCTTCGGCGAACAACAACAACTA
        ************************************************************

Pin     GTGCAGCCCAATGCTAATACTCACACTGGGTTACTATATCAGTCTCTCCAGCTCAACAAC
Sep     GTGCAGCCCAATGCTAATACTCACACTGGGTTACTATATCAGTCTCTCCAGCTCAACAAC
        ************************************************************

Pin     AGTTTCCGCCTTCAGCCCGCTCAGCCTAACCTCCAAGACCCCAGTTCCTCCACCCTTGCC
Sep     AGTTTCCGCCTTCAGCCCGCTCAGCCTAACCTCCAAGACCCCAGTTCCTCCACCCTTGCC
        ************************************************************

Pin     CTCCTCCAATCGTATGGTATATATGATACATACGTATACGATGCATTTCAAGGGATTGTT
Sep     CTCCTCCAATCGTATGGTATATATGATACATACGTATACGATGCATTTCAAGGGATTGTT
        ************************************************************

Pin     TGGTTGCATCTTTCCCACTTAGCATTTTAA
Sep     TGGTTGCATCTTTCCCACTTAGCATTTTAA
        ******************************
```

Figure 5.6: cDNA sequence of FBP24 in Pin and *sepaloid.* Alginment of FBP24 cDNA sequences extracted and assembled from WT Pin (Pin) and *sepaloid* (Sep) flower buds.

Following the initial identification of the 51 genes within the assembled *Primula* contig, each was successfully annotated and a predicted genomic DNA sequence was generated for each gene. These predictions are summarised in Table 5.2 and the predicted sequence of these genes can be seen in Appendix C. Among these, two genes (*PvG25* and *PvG35*) show a high number of Ns in their genomic DNA sequence, the result of uncertainty when the bases were called during DNA sequencing. In the instance of *PvG35*, these are seen in the 500bp following the gene and contained within the 3' UTR and, subsequently, this region of the gene cannot be fully analysed. This region could be easily clarified by repeated sequencing the region. In contrast to this, *PvG25* contains a large number of Ns within the single intron that was identified for this gene. Although this has not affected the identification of the genes coding sequence, resequencing of this area would provide further clarification.

The sequence of this gene also retains a level of uncertainty due to its position within the sequence. As seen in Appendix C, the final bases of the third exon are shown as XXX, the marker used to indicate the boundary between the 2nd and 3rd contigs within the assembled *Primula* sequence. As described in 4.2.2.ii, this is a region of uncertainty within the assembled sequence and, whilst this does not affect the identified coding sequence of *PvG25*, it does affect the sequence of the 3' UTR shown in Appendix C.

As described in 5.2.2.iii, a Northern blot was planned for use in an expression analysis of *PvG1-51*. Although time constraints meant that this analysis was not performed, the PCR shown in Figure 5.5 was performed to amplify the 3' end of each gene as well as a part of the 3' UTR and a product was obtained for each of the 51 genes. Although this primarily provides evidence for the presence of the genes

within the *Primula* contig, it also strengthens the credibility of the sequence as a correct assembly, particularly when these genes coincided with the joining of sequences to form the contig, described in Chapter 4. This is particular significance in the instance of *PvG35* where, as discussed above, the final exon of the gene lies close to the boundary between Seq2 and Seq3. The successful amplification of a product therefore suggests that, if a gap does exists between Seq2 and Seq3 in the assembled contig, it can only be small.

In the example of *PvG46*, described above in 5.2.2, the genomic sequence of the *Primula* homologue of the *Petunia* gene *FBP24*, is derived from the *Primula* genomic sequence. As seen in Figure 5.1, the sequences originally identified from the BLASTX search were highlight in colours that corresponded to different matches from the *Primula* query. Among these highlighted regions, some amino acids in the sequence have not been highlighted, though some of these have later been incorporated as extra amino acids have been incorporated into these preliminary exons.

When the preliminary exons highlighted Figure 5.1 were identified in the translated *Primula* sequence, not all were found within the same open reading frame. For example, in *PvG46*, these exons were found in both the 2nd and 3rd open reading frames. In other instances, however, exons were identified throughout all three frames or, conversely, all exons were found within the same frame. Using the GT-AG rule to identify intron/exon boundaries allowed for these preliminary exons to be lengthened or shortened to the appropriate length. In instances such as those seen in Figure 5.1 where the *Primula* exons appeared to be shorter than the subject species' exons, a lengthening of the working exons was favoured. Although this resulted in exons that were more similar in length to those in the subject species, it is possible

that the intron sequence of some *Primula* genes has been included within their coding sequences shown in Appendix C. Similarly, it is possible that coding sequence has been including within the intron sequences shown for each gene. For many of the genes annotated in the way described in 5.2.2, some change in exon length was necessary in order to ensure the GT-AG rule was adhered to without any shift in open reading frame. Many of these changes in length involved a very small number of bases, though some examples involved a much greater change in exon length, allowing a greater margin for error as described above. Similar errors may also have occurred when the lengths of the first and final exons were adjusted to reach start and stop codons respectively. Therefore, further work should proceed with the reservation that the genomic structures of genes annotated in this chapter are predictions and have not been confirmed. Whilst the presence of the genes shown in Table 5.1 is not in doubt, it should be borne in mind that errors may have been introduced due to the sole use of the GT-AG rule alone in predicting intron/exon boundaries.

Although it is difficult to determine if errors such as these occurred in the annotation of the 51 *Primula* genes that were identified, independent repetition of the annotation process could provide supporting evidence. Similarly, a cDNA database, generated in support of a *P. vulgaris* genome sequencing project and under development at the time of writing, could also be used to verify the predictions made in this chapter.

The data presented in this chapter demonstrates that the area immediately surrounding the Pin allele of the *Primula S* locus contains a wide variety of genes fulfilling a wide range of functions. However, it is possible that more genes may be present than those that have been identified. As described in 5.1, the assembled *Primula* sequence within which these genes were identified consists of the three

contigs, joined and treated as a single consecutive sequence. As a result, it is possible that more genes could be found if any of the genome has been lost if the contigs were joined prematurely. Whilst data such as that shown in Figure 5.5 suggests only a small gap may exist between Seq2 and Seq3 of the assembled contig, the size of the gap between Seq1 and Seq2 remains unknown. In addition to this, as the sequence has been assembled using genomic DNA from Pin individuals, it is possible that differences may be seen if the same analysis were made on Thrum genomic DNA. While it is unlikely that the genes identified would serve different functions it is possible that polymorphisms might exist between the two forms. This is already known to occur in genes such as *PvGLO, PvSLL1* and *PvSLL2* (Li *et al*., 2007, 2008).

The characterisation of this region also allows for comparisons to be drawn between *Primula* and other plant species. As discussed above, it is known that the system limiting recombination of the S locus must degenerate within the region spanned by the 51 genes identified in this chapter, though it is not known if the structure of this region and the order of the genes within it is a consequence of the *S* locus' presence or if it pre-existed the locus. However, it may be possible to answer this question if any level of synteny can be determined between this region of the *P.* vulgaris genome and those of closely related species, and this will be addressed in Chapter 6.

CHAPTER SIX

Syntenic mapping of *Primula vulgaris* genes

6.1 Introduction

The identification and annotation of 51 genes within the sequence assembled in Chapter 4 has provided an insight into the nature of the genes in the immediate surroundings of the *Primula vulgaris S*-locus. In addition to identifying the function of the genes, it is also important to explore the order of the genes within this region to gain insight into their evolutionary relationships.

It is known already that few recombination events take place within the *S*-locus itself and evidence suggests that some of the surrounding genes, such as *PvSLL1* and *PvGLO,* possess specific Pin and Thrum alleles (Li *et al*., 2010; Li *et al*., 2011). Although no recombinants between the *S* locus and *PvSLL1* have been identified, recombination is known to occur between the *S* locus and *PvGLO.* As both of these genes can be found within the assembled *Primula* sequence, with *PvG2* identified as *PvSLL1* and *PvG49* as *PvGLO*, this would suggest that some of the other genes in this region are also likely to be protected against any recombination events, while others are not.

The evolution of the *S*-locus has been instrumental in the development of the floral morphologies seen in *Primula* species as a part of their self-incompatibility systems. The locus itself is thought to consist of the three loci G, P and A (Ernst 1933, 1936b, 1955) and the preservation of the area immediately surrounding these genes from recombination has been key to the conservation of the *S*-locus as a whole. However the extent to which this unknown mechanism, preventing recombination among the key genes of the locus, extends beyond *G* and *A* is unknown.

Another question yet to be answered regards the point in evolutionary history at which the *S* locus genes converged within this region of the *P. vulgaris* genome. As *Primula* evolved, genes *PvG1-51* must have settled, along with the *S* locus genes, within the genome to form the gene order seen in Chapter 4. However, it is unknown whether *PvG1-51* converged around the pre-existing *S* locus or if the *S* locus genes moved into this region after *PvG1-51*. If it can be shown that this gene order is shared with other close relatives of *P. vulgaris*, either with a different SI system or no SI system, this would suggest that the gene order seen in Chapter 4 predates the arrival of the *S* locus genes within this region and that the *Primula S* locus developed after the *Primulaceae* diverged from a common ancestor.

In order to determine this, homologues of *PvG1-51* will be identified in other plant species and their locations within these other genomes will be determined. In order to gain a representative view throughout the range of Primula-related species, the Eudicot species *Arabidopsis thaliana, Solanum lycopersicum* and *Medicago truncatula* were chosen for comparison. The positions of these species within the phylogenetic tree of the Core Eudicots are shown in Figure 6.1.

In addition to these three species, *Oryza sativa* will also be used for comparison. As a monocotyledonous species, *O. sativa* was selected to provide a contrast to the four eudicotyledonous species. With reference to Figure 6.1 therefore, it was predicted that whilst *Solanum* would show the highest level of synteny and preservation of gene order, and *Oryza* would show the least. As can be seen in Figure 6.1, *Medicago* and *Arabidopsis* both lie a similar distance from *Primula* making any prediction as to which is the more closely related species to *P. vulgaris* difficult. However, any preservation of gene order that is observed in comparisons with *Primula* would allow this question to be answered.

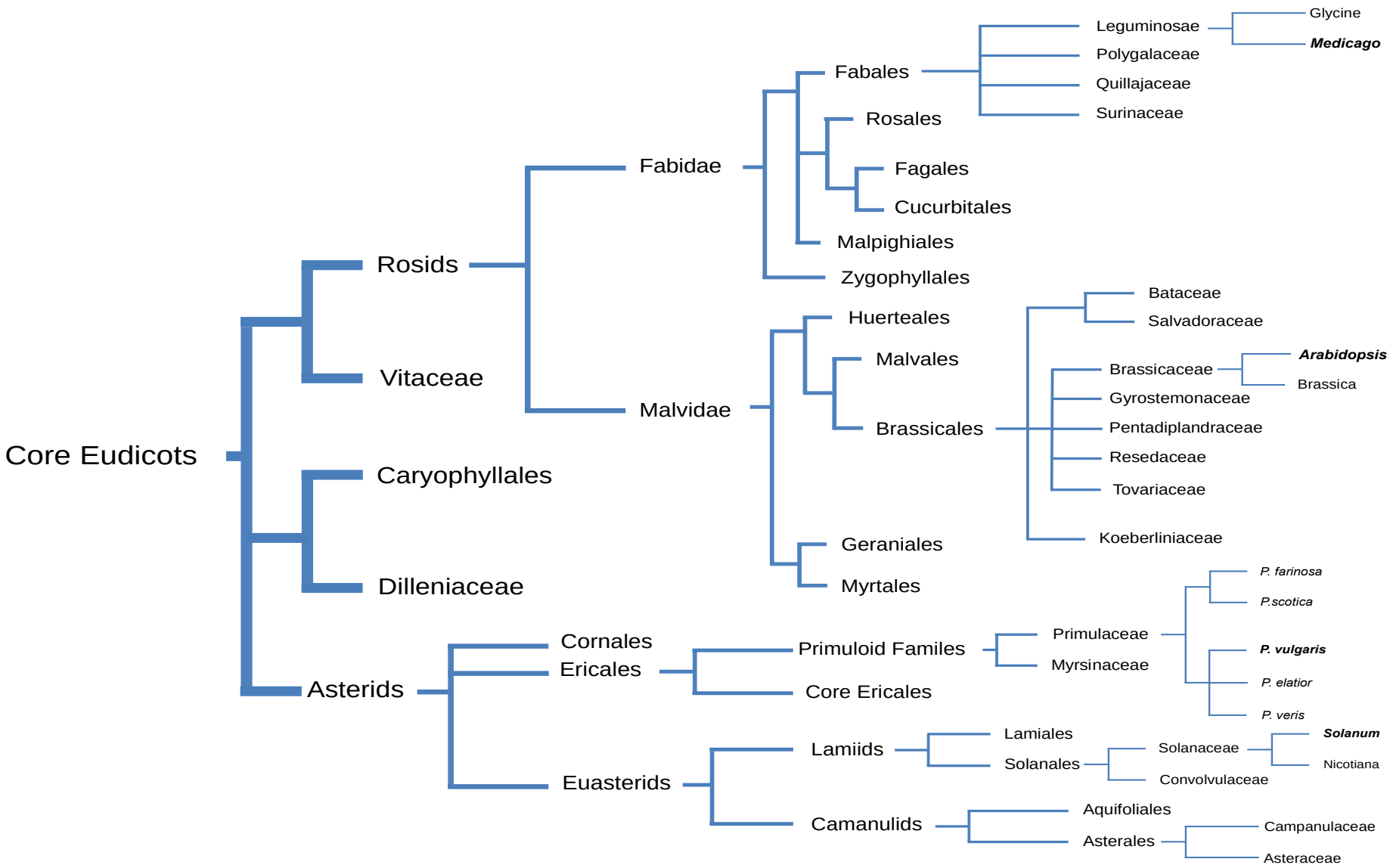


Figure 6.1: Phylogenetic tree showing a selection of genera from the Core Eudicots. The positions of *Medicago truncatula*, *Arabidopsis thaliana*, *Primula vulgaris* and *Solanum lycopersicum* are shown in bold. Tree shows only partial data of Eudicot genera so as to highlight the genera being examined and their locations relative to each other (Adapted from www. phytozome.net).

6.2 Results

6.2.1 Identification of homologous genes

In order to identify homologous genes from different species, the amino acid sequences of *PvG1-51*, annotated in Chapter 5, were used to perform BLASTP searches against the following databases:

- *Arabidopsis thaliana* genes were identified by searching the TAIR database
- *Solanum lycopersicum*, *Medicago truncatula* and *Oryza sativa* genes were identified by searching the species-specific areas of the Phytozome database.

The translated nucleotide sequence of each *P. vulgaris* gene (*PvG1*-51) was individually blasted against each species-specific database. Tables 6.1, 6.2, 6.3 and 6.4 show the results of each set of BLASTP searches. For each BLASTP search result, the subject's locus name and location within the subject genome was recorded, as well as the length of the amino acid sequence identified. In addition to this, Tables 6.1, 6.2, 6.3 and 6.4 also record the orientation of the subject sequence relative to the query sequence. +/+ indicates that the subject sequence was found in the same orientation as the query whereas +/- indicates that the subject was in the reverse complement orientation to the query sequence.

Table 6.1: Homologous genes identified in *Arabidopsis thaliana.* Results of BLASTP searches, using translated *Primula vulgaris* queries to search the TAIR database and identify homologous genes from *Arabidopsis thaliana*.

	Primula vulgaris				***Arabidopsis thaliana***				
Gene #	**Function**	**Location**	**Length (AA)**	**Orientation**	**Locus Name**	**Chromosome**	**Location**	**Length (AA)**	**Orientation**
PvG1	ARS Binding Protein	5216-8428	83	+/+	At2G07440.1	2	3093821-3094750	136	+/-
PvG2	SLL1 Protein	24498-24686	92	+/+	At1G72020.1	1	27109291-27110431	97	+/-
PvG3	Neutral/Alkaline Invertase	31510-37590	567	+/-	At4G09510.1	4	6021164-6023873	558	+/-
PvG4	Retroelement pol polyprotein	49285-53606	1463	+/-	At1G21280.1	1	7447490-7448463	237	+/-
PvG5	Disulphide-Isomerase-like protein	58838-66654	409	+/+	At1G35620.1	1	13156368-13158467	440	+/+
PvG6	E3 Ubiquitin-protein ligase RNF167-like	67922-73538	419	+/-	At1G71980.1	1	27097903-27100139	448	+/+
PvG7	Predicted Protein	79379-80266	296	+/-	At5G28150.1	5	10135434-10136977	289	+/+
PvG8	Serine/threonine Protein KinaseWNK1-like	97383-103102	709	+/+	At3G04910.1	3	1354635-1358211	700	+/+
PvG9	Cytochrome P450.1	108359-111035	497	+/+	At2G45560.1	2	18776052-18778510	512	+/-
PvG10	Cytochrome P450-2	114043-115977	498	+/+	At1G33720.1	1	12220897-12224000	511	+/-
PvG11	Uncharacterised Protein	117891-118502	204	+/+	At1G22680.1	1	8024967-8026356	185	+/-

PvG12	Unknown Protein	119344-119613	90	+/+	At1G48410.2	1	17886098-17892586	1050	+/-
PvG13	Squalene Epoxidase	130031-134460	556	+/-	At1G58440.1	1	21713842-21717290	531	+/-
PvG14	Chalcone synthase	144607-146146	384	+/+	At5G13930.1	5	4488688-4490264	395	+/+
PvG15	Hypothetical Protein	155041-155733	231	+/+	AtMG00860.1	Mitochondria	235916-236392	158	+/-
PvG16	Long Chain Acyl-CoA synthetase 9	161609-166651	725	+/+	At1G77590.1	1	29148256-29152315	691	+/-
PvG17	Uncharacterised Protein	171165-173990	220	+/+	At1G21830.1	1	7661118-7662608	206	+/-
PvG18	Chlorophyllide a oxygenase	183416-188994	521	+/+	At1G44446.	1	16848359-16851224	536	+/-
PvG19	Uncharacterised Protein	189753-190058	102	+/-	At1G44414.1	1	16847781-16848086	101	+/+
PvG20	Delta-aminolevulinic Acid Dehydratase	191502-194207	374	+/-	At1G69740.1	1	26231804-26234963	430	+/+
PvG21	Zinc Finger Protein	199632-201671	367	+/+	At5G66730.1	5	26641652-26644402	500	+/-
PvG22	Uncharacterised Protein	214537-215577	162	+/+	At1G55080.1	1	20553011-20554254	244	+/-
PvG23	Pentatricopeptide repeat containing protein	219426-222038	706	+/-	At1G17630.1	1	6064525-6066720	731	+/+
PvG24	Uncharacterised Chaperonin Protien	225329-229433	501	+/-	At3G13860.1	3	4561517-4565279	572	+/-
PvG25	Hypothetical Protein	237212-238163	289	+/+	At4G23160.1	4	12129485-12134187	1262	+/+
PvG26	Peroxidase 16	241990-245513	319	+/-	At2G18980.1	2	8233335-8235316	323	+/-

PvG27	Villin-4-like Actin Binding Protein	255862-267978	1064	+/-	At4G30160.2	4	14753349-14760189	983	+/+
PvG28	Predicted Zinc Finer MYM-type protein	273574-275370	616	+/-	At3G29765.1	3	11595467-11597077	536	+/-
PvG29	Protein Disulphide-Isomerase-Like	284536-291729	542	+/-	At1G21750.1	1	7645700-7648841	501	+/+
PvG30	Uncharacterised Protein	294637-301241	949	+/-	At1G21740.1	1	7641580-7645078	953	+/+
PvG31	CTV.20 RNA Binding Protein	312367-317949	1416	+/-	At5G48130.1 ***(V.Poor)***	5	19516102-19518513	625	+/+
PvG32	Hydrolase	318968-320023	352	+/+	At2G13770.1	2	5736570-5737847	343	+/+
PvG33	Non-LTR retroelement reverse transcriptase	323682-325567	596	+/-	At4G29090.1	4	14333528-14335255	575	+/+
PvG34	Hypothetical Protein (Transposase)	332170-334027	597	+/+	At3G42170.1	3	14320952-14324069	696	+/+
PvG35	NAC Domain Containing Protein 82	343247-343564	106	+/+	At5G09330.1	5	2892365-2895421	489	+/-
PvG36	Aldehyde dehydrogenase family 3 member H1-like	348276-353864	493	+/+	At1G44170.1	1	16796400-16800321	484	+/-
PvG37	Aspartic proteinase ASP1- like	359616-363145	358	+/+	At1G44130.1	1	16787508-16789318	405	+/-
PvG38	Ubiquitin Protein Ligase	364431-373537	2119	+/-	At1G77460.1	1	29103763-29111921	2136	+/+
PvG39	NAC Domain-containing protein 2	380639-383458	290	+/-	At1G01720.1	1	268330-269819	289	+/+
PvG40	Root Specific Metal	391053-	544	+/-	At1G15960.1	1	5481665-	527	+/-

	Transporter	396282					5485082		
PvG41	60S Ribosomal export protein NMD3-like	398906-399172	89	+/-	At2G03820.1	2	1164957-1167029	516	+/-
PvG42	Cyclin-A1-1-like	407699-410672	389	+/+	At1G44110.1	1	16774865-16777247	460	+/-
PvG43	Amino Acid Permease 2	420331-423218	485	+/+	At1G77380.1	1	29074888-29077390	476	+/-
PvG44	Integrase catalytic region Zinc Finger, CCHC-type aspartic peptidase	429089-433960	1252	+/+	At1G64190.1 ***(V.Poor)***	1	23825328-23827136	487	+/-
PvG45	NAD Kinase 2	435960-441784	890	+/-	At1G21640.2	1	7588414-7592831	999	+/+
PvG46	Floral Binding Protein 24	451905-456773	309	+/+	At5G23260.2	5	7836096-7838505	252	+/+
PvG47	Uncharacterised WW domain containing protein	458737-465809	461	+/-	At2G41020.1	2	17117263-17121119	463	+/+
PvG48	Retrotransposon Polyprotein	473910-476081	546	+/-	*At4G23160.1* ***(V.Poor-Same as PvG25)***	*4*	*12129485-12134187*	*1262*	+/+
PvG49	Glo Protein	481859-486579	244	+/+	At5G20240.1	5	6829042-6831515	208	+/+
PvG50	UDP-n-acetylglucosamine pyrophosphorylase	493319-501895	804	+/+	At5G52560.1	5	21330639-21334811	614	+/+
PvG51	2-oxoisovalerate dehydrogenase	505633-509265	448	+/+	At5G09300.1	5	2884179-2886863	472	+/-

Table 6.2: Homologous genes identified in *Solanum lycopersicum.* Results of BLASTP searches, using translated *Primula vulgaris* queries to search the Phytozome database and identify homologous genes from *Solanum lycopersicum.*

	Primula vulgaris				***Solanum lycopersicum***				
Gene #	**Identity**	**Location**	**Length (AA)**	**Orientation**	**Locus Name**	**Chromosome**	**Location**	**Length (AA)**	**Orientation**
PvG1	ARS Binding Protein	5216-8428	83	+/+					
PvG2	SLL1 Protein	24498-24686	92	+/+	Solyc06g065180.2	6	37028954-37032350	88	+/+
PvG3	Neutral/Alkaline Invertase	31510-37590	567	+/-	Solyc06g065210.2	6	37049546-37053685	551	+/-
PvG4	Retroelement pol polyprotein	49285-53606	1463	+/-	Solyc04g025890.1	4	23026497-23026784	95	+/+
PvG5	Disulphide-Isomerase-like protein	58838-66654	409	+/+	Solyc11g019920.1	11	9781305-9788278	435	+/+
PvG6	E3 Ubiquitin-protein ligase RNF167-like	67922-73538	419	+/-	Solyc06g065330.2	6	37127159-37132449	306	+/-
PvG7	Predicted Protein	79379-80266	296	+/-	Solyc01g097790.2	1	80260882-80262313	299	+/-
PvG8	Serine/threonine Protein KinaseWNK1-like	97383-103102	709	+/+	Solyc01g097840.2	1	80304661-80308285	748	+/+
PvG9	Cytochrome P450.1	108359-111035	497	+/+	Solyc08g080380.2	8	60845204-60847167	496	+/+
PvG10	Cytochrome P450-2	114043-115977	498	+/+	Solyc08g080380.2	8	60845204-60847167	496	+/+
PvG11	Uncharacterised Protein	117891-118502	204	+/+	Solyc06g065340.1	6	37149542-37150216	224	+/-

PvG12	Unknown Protein	119344-119613	90	+/+	Solyc03g098280.2	3	54075745-54082377	980	+/+
PvG13	Squalene Epoxidase	130031-134460	556	+/-	Solyc00g085070.2	0	151749121 5178624	463	+/-
PvG14	Chalcone synthase	144607-146146	384	+/+	Solyc09g091510.2	9	66123066-66125217	389	+/+
PvG15	Hypothetical Protein	155041-155733	231	+/+	Solyc00g010540.1	0	9815548-9816573	341	+/-
PvG16	Long Chain Acyl-CoA synthetase 9	161609-166651	725	+/+	Solyc11g018580.1	11	8753165-8759597	610	+/+
PvG17	Uncharacterised Protein	171165-173990	220	+/+	Solyc11g013450.1	11	6470193-6472721	220	+/+
PvG18	Chlorophyllide a oxygenase	183416-188994	521	+/+	Solyc11g012850.1	11	5644237-5648033	535	+/-
PvG19	Uncharacterised Protein	189753-190058	102	+/-	Solyc06g060300.1	6	34672906-34673223	105	+/+
PvG20	Delta-aminolevulinic Acid Dehydratase	191502-194207	374	+/-	Solyc08g069030.2	8	55322764-55332861	430	+/+
PvG21	Zinc Finger Protein	199632-201671	367	+/+	Solyc03g121660.2	3	63812805-63815522	542	+/-
PvG22	Uncharacterised Protein	214537-215577	162	+/+	Solyc02g069520.2	2	33969549-33971170	205	+/+
PvG23	Pentatricopeptide repeat containing protein	219426-222038	706	+/-	Solyc06g062610.1	6	35917241-35919433	705	+/+
PvG24	Uncharacterised Chaperonin Protien	225329-229433	501	+/-	Solyc03g121640.2	3	63788759-63796170	573	+/+
PvG25	Hypothetical Protein	237212-238163	289	+/+	Solyc01g034160.1	1	36659262-36660140	292	+/-
PvG26	Peroxidase 16	241990-245513	319	+/-	Solyc07g017880.2	7	8260969-8263025	329	+/-

PvG27	Villin-4-like Actin Binding Protein	255862-267978	1064	+/-	Solyc02g021420.2	2	13328830-13352997	973	+/-
PvG28	Predicted Zinc Finer MYM-type protein	273574-275370	616	+/-	Solyc10g045680.1	10	30482975-30483496	173	+/+
PvG29	Protein Disulphide-Isomerase-Like	284536-291729	542	+/-	Solyc06g060290.2	6	34649921-34655100	438	+/-
PvG30	Uncharacterised Protein	294637-301241	949	+/-	Solyc06g060270.2	6	34636335-34648511	1014	+/+
PvG31	CTV.20 RNA Binding Protein	312367-317949	1416	+/-	Solyc03g115130.2	3	58980489-58983849	303	+/+
PvG32	Hydrolase	318968-320023	352	+/+	Solyc04g040030.1	4	30759231-30759657	72	+/-
PvG33	Non-LTR retroelement reverse transcriptase	323682-325567	596	+/-	Solyc03g077970.1	3	42200408-42201168	215	+/+
PvG34	Hypothetical Protein (Transposase)	332170-334027	597	+/+	Solyc10g007810.2	10	2028853-2031189	669	+/-
PvG35	NAC Domain Containing Protein 82	343247-343564	106	+/+	Solyc04g016080.1	4	6781720-6791327	1231	+/+
PvG36	Aldehyde dehydrogenase family 3 member H1-like	348276-353864	493	+/+	Solyc06g060250.2	6	34593565-34601818	474	+/-
PvG37	Aspartic proteinase ASP1- like	359616-363145	358	+/+	Solyc06g009110.2	6	3053791-3057937	420	+/-
PvG38	Ubiquitin Protein Ligase	364431-373537	2119	+/-	Solyc11g017460.1	11	8409733-8419900	2133	+/+
PvG39	NAC Domain-containing protein 2	380639-383458	290	+/-	Solyc06g060230.2	6	34577474-34578909	296	+/-
PvG40	Root Specific Metal	391053-	544	+/-	Solyc11g018530.1	11	8641837-	530	+/-

	Transporter	396282					8646829		
PvG41	60S Ribosomal export protein NMD3-like	398906-399172	89	+/-	Solyc06g053800.1	6	33148340-33149857	505	+/-
PvG42	Cyclin-A1-1-like	407699-410672	389	+/+	Solyc11g005090.1	11	69680-73275	490	+/-
PvG43	Amino Acid Permease 2	420331-423218	485	+/+	Solyc06g060110.2	6	34421106-34423721	471	+/-
PvG44	Integrase catalytic region Zinc Finger, CCHC-type aspartic peptidase	429089-433960	1252	+/+	Solyc00g025650.1	0	12289922-12291544	490	+/+
PvG45	NAD Kinase 2	435960-441784	890	+/-	Solyc06g060060.2	6	34359018-34368653	458	+/-
PvG46	Floral Binding Protein 24	451905-456773	309	+/+	Solyc11g005120.1	11	107329-109329	238	+/-
PvG47	Uncharacterised WW domain containing protein	458737-465809	461	+/-	Solyc11g005110.1	11	92574-105206	523	+/-
PvG48	Retrotransposon Polyprotein	473910-476081	546	+/-	Solyc12g009540.1	12	2785567-2787063	498	+/+
PvG49	Glo Protein	481859-486579	244	+/+	Solyc06g059970.2	6	34286205-34289235	214	+/-
PvG50	UDP-n-acetylglucosamine pyrophosphorylase	493319-501895	804	+/+	Solyc04g058070.2	4	54328964-54342003	617	+/+
PvG51	2-oxoisovalerate dehydrogenase	505633-509265	448	+/+	Solyc04g063350.2	4	54581013-54588153	472	+/+

Table 6.3: Homologous genes identified in *Medicago truncatula.* Results of BLASTP searches, using translated *Primula vulgaris* queries to search the Phytozome database and identify homologous genes from *Medicago truncatula.*

	Primula vulgaris				***Medicago truncatula***				
Gene #	**Identity**	**Location**	**Length (AA)**	**Orientation**	**Locus Name**	**Chromosome**	**Location**	**Length (AA)**	**Orientation**
PvG1	ARS Binding Protein	5216-8428	83	+/+	Medtr5g087330.1	5	36814906-36816580	308	+/-
PvG2	SLL1 Protein	24498-24686	92	+/+					
PvG3	Neutral/Alkaline Invertase	31510-37590	567	+/-	Medtr1g096140.1	1	27708256-27713168	555	+/-
PvG4	Retroelement pol polyprotein	49285-53606	1463	+/-	Medtr2g065630.1	2	21228156-21229889	475	+/-
PvG5	Disulphide-Isomerase-like protein	58838-66654	409	+/+	Medtr4g059450.1	4	18197853-18203134	583	+/+
PvG6	E3 Ubiquitin-protein ligase NF167-like	67922-73538	419	+/-	Medtr5g024730.1	5	9683574-9684454	215	+/+
PvG7	Predicted Protein	79379-80266	296	+/-	Medtr1g081260.1	1	20697153-20704037	336	+/-
PvG8	Serine/threonine Protein KinaseWNK1-like	97383-103102	709	+/+	Medtr1g081330.1	1	20740323-20743528	742	+/+
PvG9	Cytochrome P450.1	108359-111035	497	+/+	Medtr5g007460.1	5	11311766-133659	479	+/+
PvG10	Cytochrome P450-2	114043-115977	498	+/+	Medtr5g007460.1	5	11311766-133659	479	+/+
PvG11	Uncharacterised Protein	117891-118502	204	+/+	Medtr7g072540.1	7	19213609-19214828	226	+/-

PvG12	Unknown Protein	119344-119613	90	+/+	Medtr4g113200.1	4	38653553-38659081	876	+/+
PvG13	Squalene Epoxidase	130031-134460	556	+/-	Medtr4g092640.1	4	31797672-31801631	525	+/-
PvG14	Chalcone synthase	144607-146146	384	+/+	Medtr7g084300.1	7	25085380-25087531	391	+/-
PvG15	Hypothetical Protein	155041-155733	231	+/+	Medtr4g038660.1	4	12147449-12149686	745	+/+
PvG16	Long Chain Acyl-CoA synthetase 9	161609-166651	725	+/+	Medtr3g087980.1	3	29161083-29170645	702	+/+
PvG17	Uncharacterised Protein	171165-173990	220	+/+	Medtr3g088010.1	3	29178112-29180141	220	+/+
PvG18	Chlorophyllide a oxygenase	183416-188994	521	+/+	Medtr1g030480.1	1	8890575-8892901	233	+/-
PvG19	Uncharacterised Protein	189753-190058	102	+/-	Medtr1g030540.1	1	8910454-8912733	310	+/-
PvG20	Delta-aminolevulinic Acid Dehydratase	191502-194207	374	+/-	Medtr3g088610.1	3	29437092-29441605	413	+/-
PvG21	Zinc Finger Protein	199632-201671	367	+/+	Medtr8g017210.1	8	3637681-3640060	517	+/-
PvG22	Uncharacterised Protein	214537-215577	162	+/+	Medtr8g017180.1	8	3623684-3627972	196	+/-
PvG23	Pentatricopeptide repeat containing protein	219426-222038	706	+/-	Medtr4g113830.1	4	38969181-38971397	738	+/-
PvG24	Uncharacterised Chaperonin Protien	225329-229433	501	+/-	Medtr8g017080.1	8	3589534-3596053	576	+/+
PvG25	Hypothetical Protein	237212-238163	289	+/+	Medtr4g052100.1	4	15545727-15551605	803	+/-
PvG26	Peroxidase 16	241990-245513	319	+/-	Medtr4g127670.1	4	44452564-44454240	323	+/+
PvG27	Villin-4-like Actin	255862-	1064	+/-	Medtr2g036860.1	2	13356706-	981	+/-

	Binding Protein	267978					13367531		
PvG28	Predicted Zinc Finer MYM-type protein	273574-275370	616	+/-	Medtr5g069910.1	5	28647289-28651174	892	+/+
PvG29	Protein Disulphide-Isomerase-Like	284536-291729	542	+/-	Medtr2g094180.1	2	29162078-29166154	564	+/-
PvG30	Uncharacterised Protein	294637-301241	949	+/-	Medtr5g098980.1	5	42302962-42306877	774	+/-
PvG31	CTV.20 RNA Binding Protein	312367-317949	1416	+/-	Medtr4g038660.1	4	12147449-12149686	745	+/+
PvG32	Hydrolase	318968-320023	352	+/+	Medtr2g061140.1	2	19288663-19289949	428	+/-
PvG33	Non-LTR retroelement reverse transcriptase	323682-325567	596	+/-	Medtr5g026890.1	5	10868938-10877058	1723	+/+
PvG34	Hypothetical Protein (Transposase)	332170-334027	597	+/+	Medtr1g095710.1	1	27468770-27478574	1001	+/-
PvG35	NAC Domain Containing Protein 82	343247-343564	106	+/+					
PvG36	Aldehyde dehydrogenase family 3 member H1-like	348276-353864	493	+/+	Medtr3g088150.1	3	29252833-29256950	495	+/-
PvG37	Aspartic proteinase ASP1- like	359616-363145	358	+/+	Medtr8g094590.1	8	27299204-27302681	435	+/-
PvG38	Ubiquitin Protein Ligase	364431-373537	2119	+/-	Medtr8g091470	8	25737476-25746785	2186	+/-
PvG39	NAC Domain-containing protein 2	380639-383458	290	+/-	Medtr3g088110.1	3	29236679-29239067	288	+/+
PvG40	Root Specific Metal Transporter	391053-396282	544	+/-	Medtr3g088440.1	3	29343080-29347956	531	+/+
PvG41	60S Ribosomal export protein NMD3-like	398906-399172	89	+/-	Medtr3g064880.1	3	20610052-20611569	505	+/+
PvG42	Cyclin-A1-1-like	407699-	389	+/+	Medtr8g095930.1	8	27976966-	531	+/+

		410672					27980407		
PvG43	Amino Acid Permease 2	420331-423218	485	+/+	Medtr8g094290.1	8	27182065-27184752	475	+/+
PvG44	Integrase catalytic region Zinc Finger, CCHC-type aspartic peptidase	429089-433960	1252	+/+	Medtr6g007870.1	6	1523549-1528281	905	+/-
PvG45	NAD Kinase 2	435960-441784	890	+/-	Medtr4g076990.1	4	24957839-24964179	523	+/+
PvG46	FBP24	451905-456773	309	+/+	Medtr1g038300.1	1	10048097-10051263	232	+/-
PvG47	Uncharacterised WW domain containing protein	458737-465809	461	+/-	Medtr6g012410.1	6	2913913-2922462	1057	+/-
PvG48	Retrotransposon Polyprotein	473910-476081	546	+/-	Medtr2g094070.1	2	29103758-29113859	2260	+/+
PvG49	Glo Protein	481859-486579	244	+/+	Medtr3g11303.1	3	40585974-40589827	229	+/+
PvG50	UDP-n-acetylglucosamine pyrophosphorylase	493319-501895	804	+/+	Medtr3g071440.1	3	22718992-22726872	868	+/-
PvG51	2-oxoisovalerate dehydrogenase	505633-509265	448	+/+	Medtr3g096390.1	3	33271901-33275050	449	+/-

Table 6.4: Homologous genes identified in *Oryza sativa.* Results of BLASTP searches, using translated *Primula vulgaris* queries to search the Phytozome database and identify homologous genes from *Oryza sativa.*

	Primula vulgaris				***Oryza sativa***				
Gene #	**Identity**	**Location**	**Length (AA)**	**Orientation**	**Locus Name**	**Chromosome**	**Location**	**Length (AA)**	**Orientation**
PvG1	ARS Binding Protein	5216-8428	83	+/+					
PvG2	SLL1 Protein	24498-24686	92	+/+	Os04g35300.1	4	21466485-21468612	98	+/-
PvG3	Neutral/Alkaline Invertase	31510-37590	567	+/-	Os02g34560.1	2	20717887-20721920	562	+/-
PvG4	Retroelement pol polyprotein	49285-53606	1463	+/-	ChrUn.fgenesh.gene.31	ChrUn	198370-206237	1847	+/-
PvG5	Disulphide-Isomerase-like protein	58838-66654	409	+/+	Os04g35290.1	4	21462033-21465044	423	+/-
PvG6	E3 Ubiquitin-protein ligase RNF167-like	67922-73538	419	+/-	Os08g01360.2	8	228215-232453	495	+/+
PvG7	Predicted Protein	79379-80266	296	+/-	Os03g59200.1	3	33711473-33713619	291	+/+
PvG8	Serine/threonine Protein KinaseWNK1-like	97383-103102	709	+/+	Os07g38530	7	23145979-23149609	704	+/+
PvG9	Cytochrome P450.1	108359-111035	497	+/+	Os03g14400.1	3	7831876-7833791	501	+/-
PvG10	Cytochrome P450-2	114043-115977	498	+/+	Os03g14400.1	3	7831876-7833791	501	+/-
PvG11	Uncharacterised Protein	117891-118502	204	+/+	Os02g34640.1	2	20776247-20777086	216	+/+
PvG12	Unknown Protein	119344-119613	90	+/+	Os04g47870	4	28426519-28441623	1118	+/-

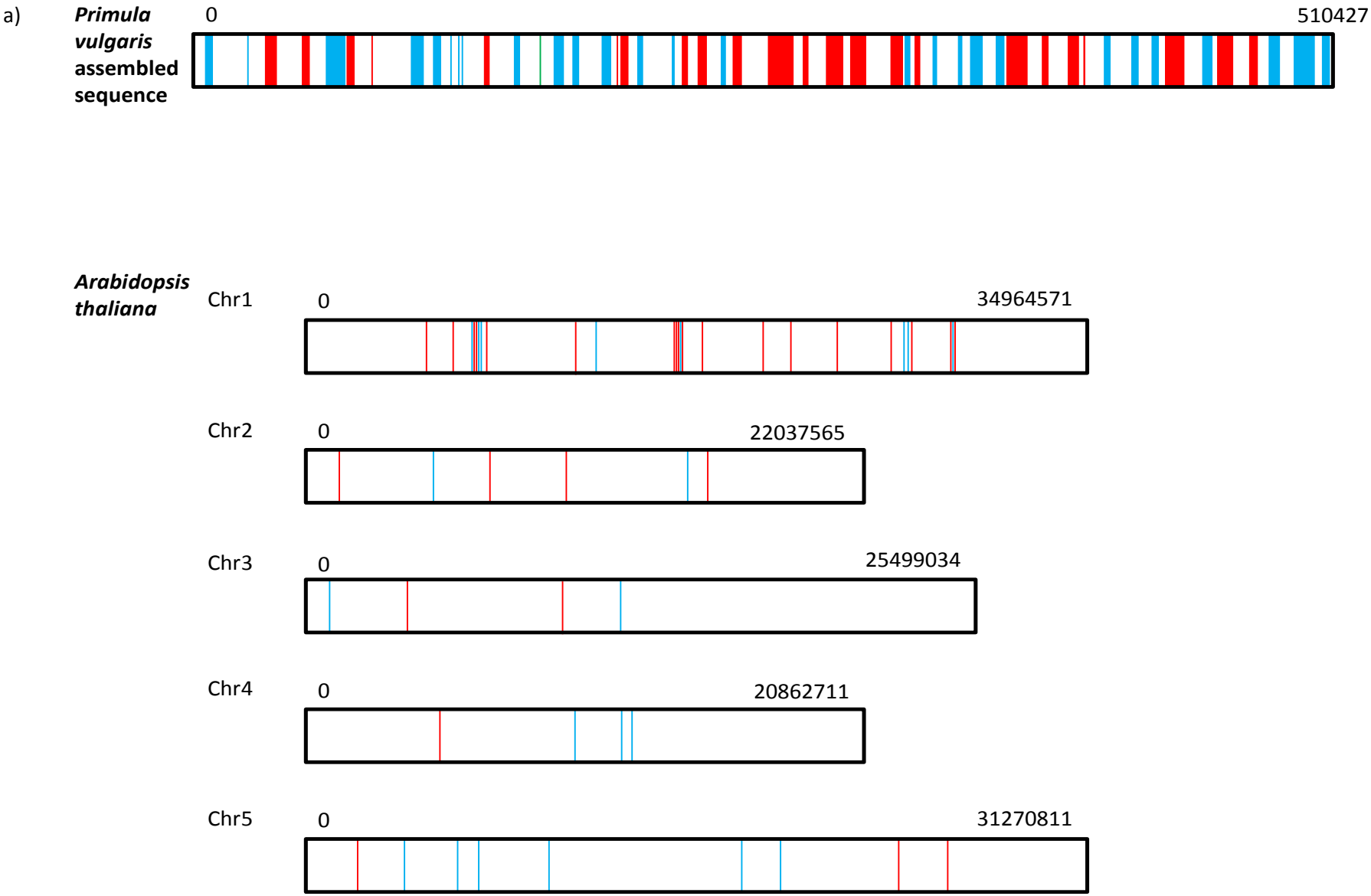
PvG13	Squalene Epoxidase	130031-134460	556	+/-	Os03g12900.1	3	6950465-6956156	582	+/-
PvG14	Chalcone synthase	144607-146146	384	+/+	Os11g32650.1	11	19277557-19281016	398	+/-
PvG15	Hypothetical Protein	155041-155733	231	+/+	ChrSy.fgenesh.gene61	ChrSy	406254-410804	1447	+/+
PvG16	Long Chain Acyl-CoA synthetase 9	161609-166651	725	+/+	Os12g07110.1	12	3483864-3489371	698	+/+
PvG17	Uncharacterised Protein	171165-173990	220	+/+	Os04g59420.2	4	35327019-35328615	227	+/+
PvG18	Chlorophyllide a oxygenase	183416-188994	521	+/+	Os10g41780.1	10	2248218-22486537	541	+/-
PvG19	Uncharacterised Protein	189753-190058	102	+/-	Os05g35970.1	5	21313235-21314150	112	+/-
PvG20	Delta-aminolevulinic Acid Dehydratase	191502-194207	374	+/-	Os06g49110.1	6	29757045-29761643	426	+/-
PvG21	Zinc Finger Protein	199632-201671	367	+/+	Os03g10140.1	3	5134268-5137506	552	+/+
PvG22	Uncharacterised Protein	214537-215577	162	+/+	Os01g31629	1	17309304-17325760	152	+/-
PvG23	Pentatricopeptide repeat containing protein	219426-222038	706	+/-	Os01g10090.1	1	5261189-5262898	569	+/-
PvG24	Uncharacterised Chaperonin Protien	225329-229433	501	+/-	Os05g46290.1	5	26835671-26840314	581	+/-
PvG25	Hypothetical Protein	237212-238163	289	+/+	ChrSy.fgenesh.gene7	ChrSy	40271-43089	889	+/+
PvG26	Peroxidase 16	241990-245513	319	+/-	Os07g02440.1	7	838070-841354	330	+/+
PvG27	Villin-4-like Actin Binding Protein	255862-267978	1064	+/-	Os06g44890.1	6	27135555-27144857	1016	+/-

PvG28	Predicted Zinc Finer MYM-type protein	273574-275370	616	+/-	Os11g39200.1	11	23342250-23344648	245	+/-
PvG29	Protein Disulphide-Isomerase-Like	284536-291729	542	+/-	Os11g09280.1	11	4971248-4975064	512	+/-
PvG30	Uncharacterised Protein	294637-301241	949	+/-	Os05g35070.1	5	20816584-20820780	872	+/-
PvG31	CTV.20 RNA Binding Protein	312367-317949	1416	+/-	Os08g39580.1	8	25043265-25047377	1275	+/-
PvG32	Hydrolase	318968-320023	352	+/+	Os05g51520.1	5	29545098-29546798	423	+/-
PvG33	Non-LTR retroelement reverse transcriptase	323682-325567	596	+/-	Os11g03360.1	11	1261956-1267499	520	+/-
PvG34	Hypothetical Protein (Transposase)	332170-334027	597	+/+	Os11g36790.1	11	21719330-21724206	1120	+/+
PvG35	NAC Domain Containing Protein 82	343247-343564	106	+/+	Os02g01490.1	2	279583-285795	1514	+/+
PvG36	Aldehyde dehydrogenase family 3 member H1-like	348276-353864	493	+/+	Os11g08300.1	11	4375281-4380044	482	+/+
PvG37	Aspartic proteinase ASP1- like	359616-363145	358	+/+	Os12g07780.1	12	3932455-3935990	451	+/+
PvG38	Ubiquitin Protein Ligase	364431-373537	2119	+/-	Os11g08090.1	11	4233460-4243344	2117	+/+
PvG39	NAC Domain-containing protein 2	380639-383458	290	+/-	Os01g66120.1	1	38398517-38401533	303	+/-
PvG40	Root Specific Metal Transporter	391053-396282	544	+/-	Os07g15370.1	7	8871436-8878905	538	+/-
PvG41	60S Ribosomal export protein NMD3-like	398906-399172	89	+/-	Os10g42320.1	10	22781929-22784426	523	+/-
PvG42	Cyclin-A1-1-like	407699-410672	389	+/+	Os01g13260.1	1	7389342-7393708	508	+/-
PvG43	Amino Acid Permease 2	420331-	485	+/+	Os05g34980.1	5	20779070-	496	+/+

		423218					20781283		
PvG44	Integrase catalytic region Zinc Finger, CCHC-type aspartic peptidase	429089-433960	1252	+/+	ChrUn.fgenesh.gene.31	ChrUn	198370-206237	1847	+/-
PvG45	NAD Kinase 2	435960-441784	890	+/-	Os11g08670.1	11	4625070-4631252	981	+/+
PvG46	FBP24	451905-456773	309	+/+	Os02g07430.1	2	3833129-3837135	260	+/-
PvG47	Uncharacterised WW domain containing protein	458737-465809	461	+/-	Os01g68760.1	1	39938753-39944888	524	+/-
PvG48	Retrotransposon Polyprotein	473910-476081	546	+/-	ChrUn.fgenesh.gene.36	ChrUn	219392-221808	778	+/-
PvG49	Glo Protein	481859-486579	244	+/+	Os01g66030.1	1	38320785-38324074	209	+/-
PvG50	UDP-n-acetylglucosamine pyrophosphorylase	493319-501895	804	+/+	Os06g48760.1	6	29508824-29515309	616	+/-
PvG51	2-oxoisovalerate dehydrogenase	505633-509265	448	+/+	Os12g08260.4	12	4209174-4213475	487	+/+

6.2.2 Mapping the loci of homologous genes

The location data recorded in Tables 6.1 – 6.4, made it possible to identify the region of the genome where each subject gene was located. Using these data, the homologous genes identified through BLASTP searches were represented in chromosomal maps, according to their locations within the subject genomes. Figure 6.2 shows the positions of the genes identified through BLASTP searches of the TAIR database within the *Arabidopsis* genome. In Figure 6.2, genes are represented by blue or red bars according to their orientation within the query or subject genomes. Genes represented in blue are in the 5' to 3' orientation whereas those in red are in the 3' to 5' orientation. The assembled *P. vulgaris* sequence is represented as a single bar at the top and the width of each band within this is in proportion to the length of the genomic sequences predicted for each gene in Chapter 5. Figure 6.2a) shows the spread of the subject genes throughout the *Arabidopsis* genome. In Figure 6.2b) lines connect the subject genes to the *Primula* query genes used to identify them within the TAIR database. Figures 6.3, 6.4 and 6.5 represent the same data for *S. lycopersicum, M. truncatula* and *O. sativa* respectively. In these figures, some genes within the *Primula* contig are represented by green or purple bands. In these instances, purple bands represent genes for which no homologue was identified. Green bands denote genes that identified subjects outside of the main chromosomes, such as ChrUn and ChrSy in *O. sativa*, discussed in 6.4.4 (Ouyang *et al.*, 2007), or the Mitochondrial genome. In each figure, numbers denote the number of base pairs in each chromosome or sequence. All chromosomes and gene positions were drawn to scale.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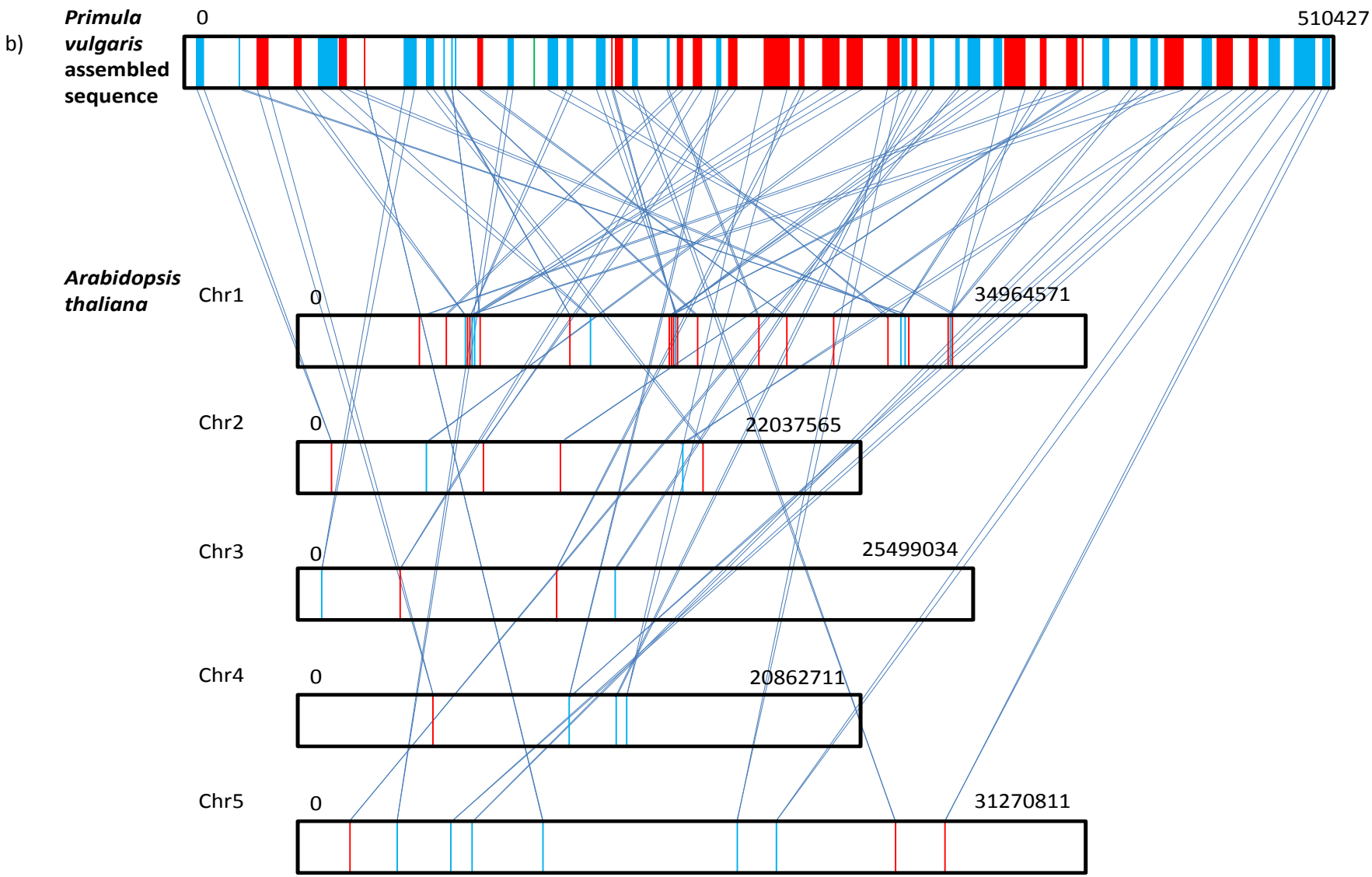
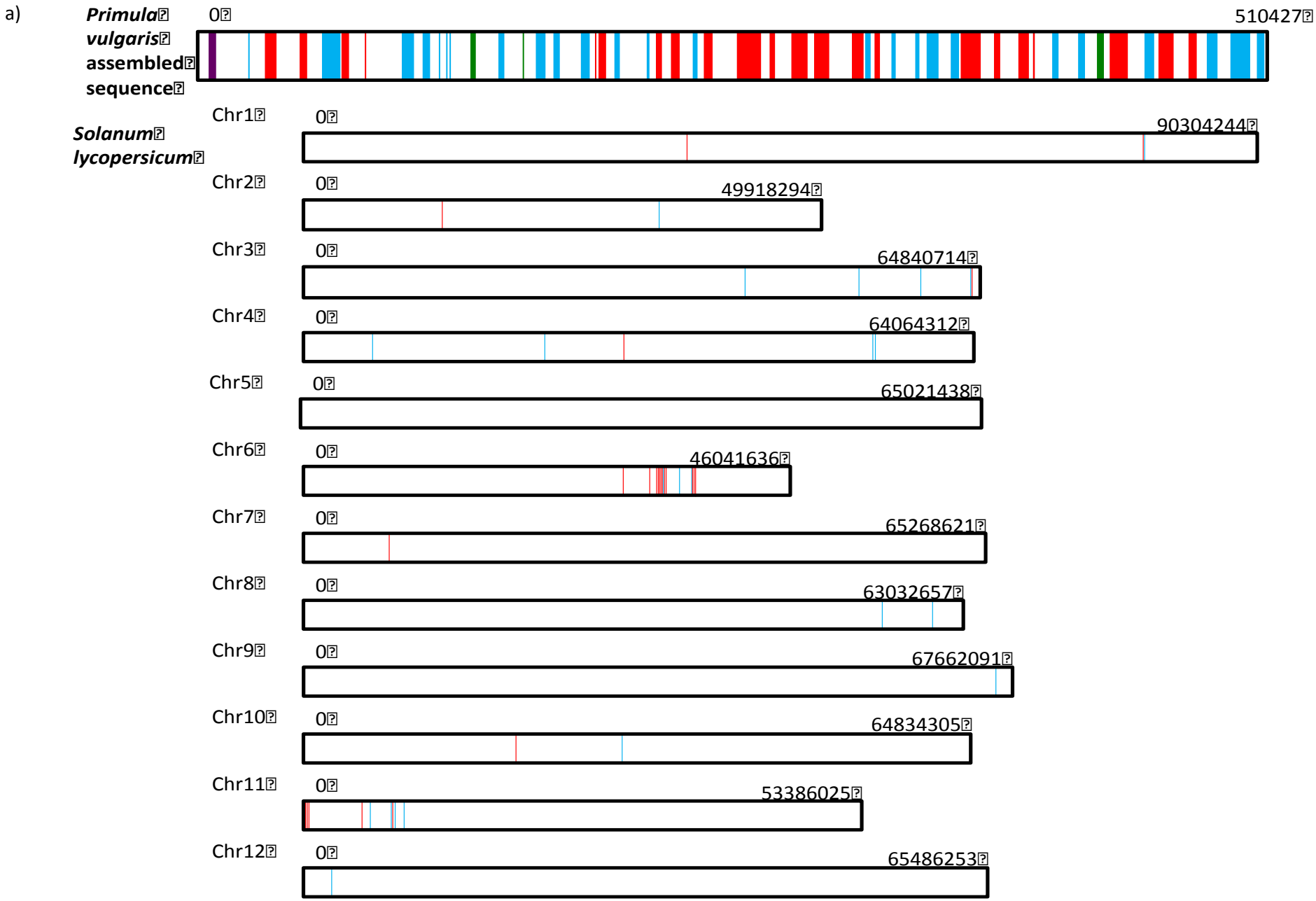


Figure 6.2: Locations of homologous genes in *A. thaliana*. Blue bars indicate genes in 5'-3' orientation and red indicates 3'-5'. a) The positions of homologous genes to those identified from the *Primula* contig in *Arabidopsis thaliana*. Numbers denote number of basepairs in chromosomes. b) Lines link the genes from the *Primula* contig to their homologues in *Arabidopsis*.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Chr4
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Chr6
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Chr7
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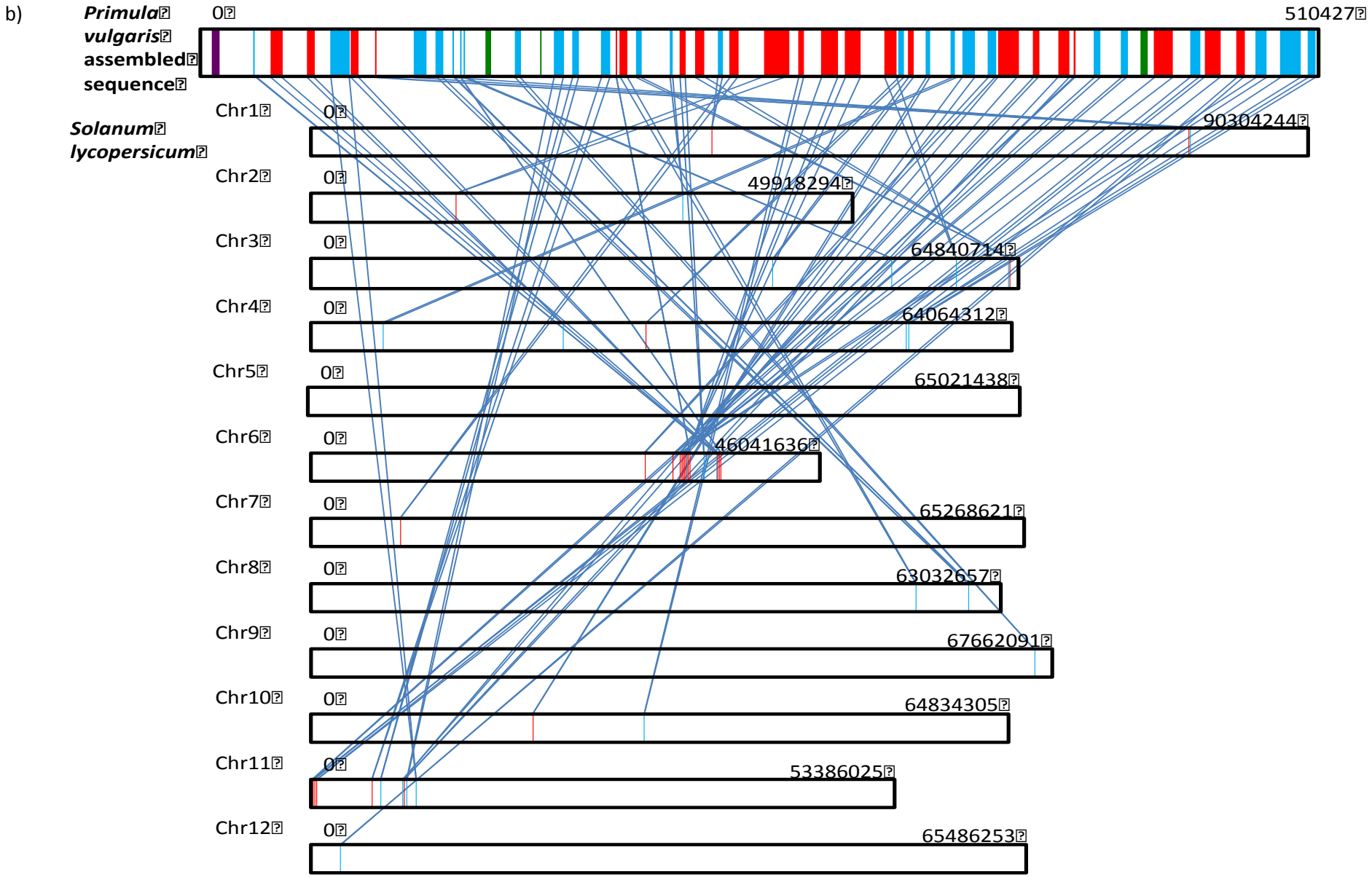
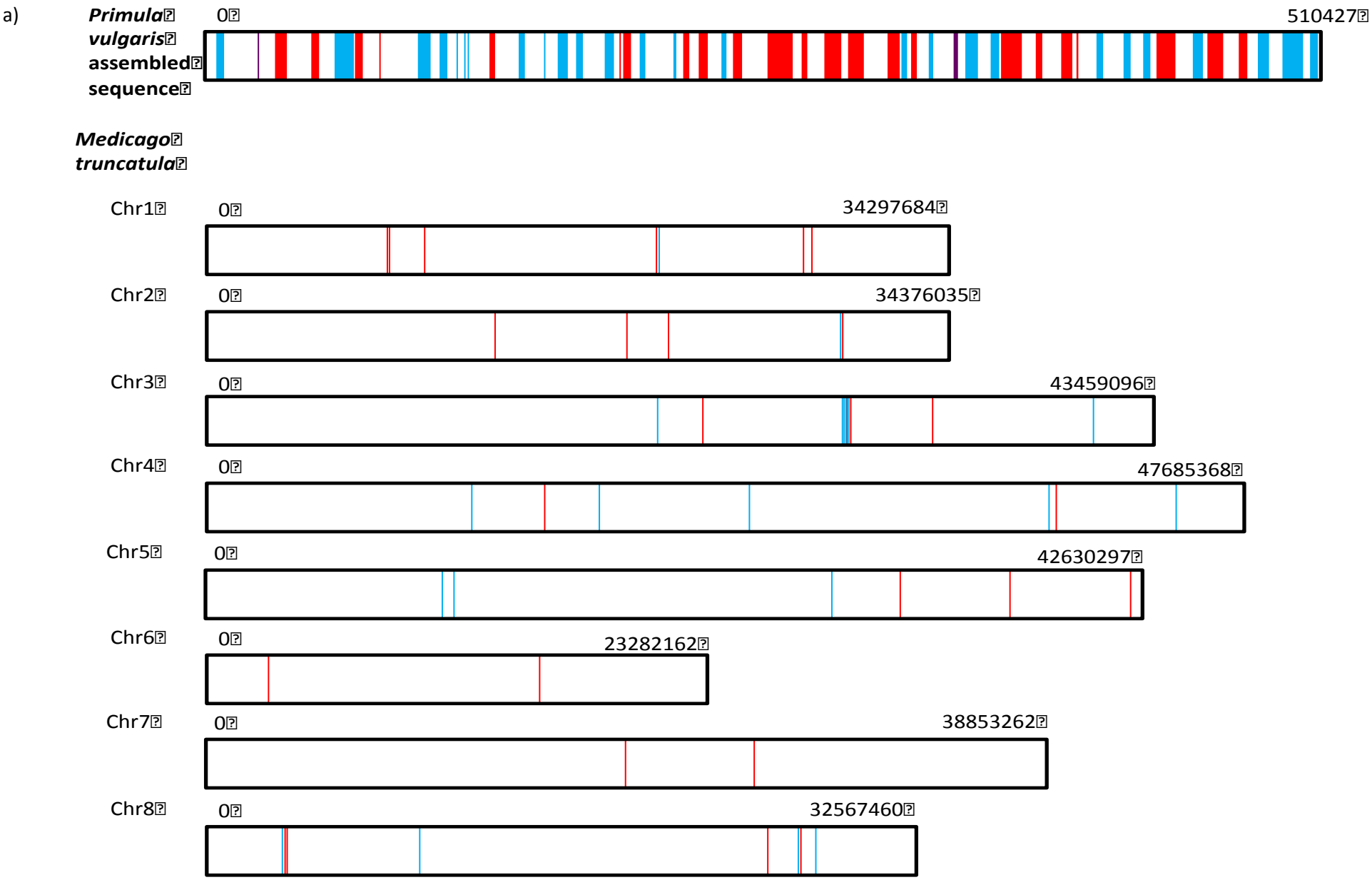


Figure 6.3: Locations of homologous genes in *S. lycopersicum.* Blue bars indicate genes in 5'-3' orientation and red indicates 3'-5'. a) The positions of homologous genes to those identified from the *Primula* contig in *Solanum lycopersicum.* b) Lines link the genes from the *Primula* contig to their homologues in *Solanum.*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Chr7
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Chr8
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b)

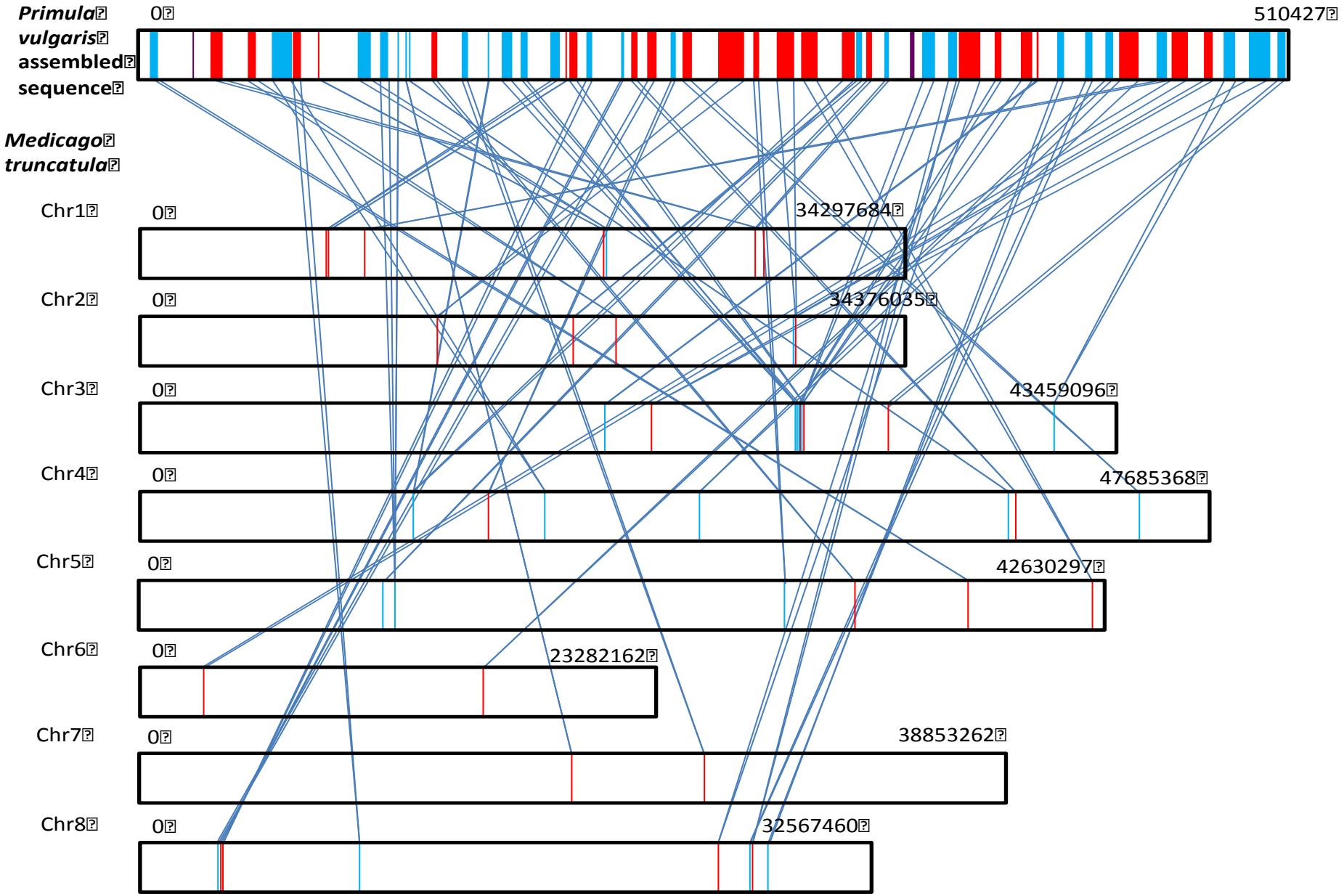
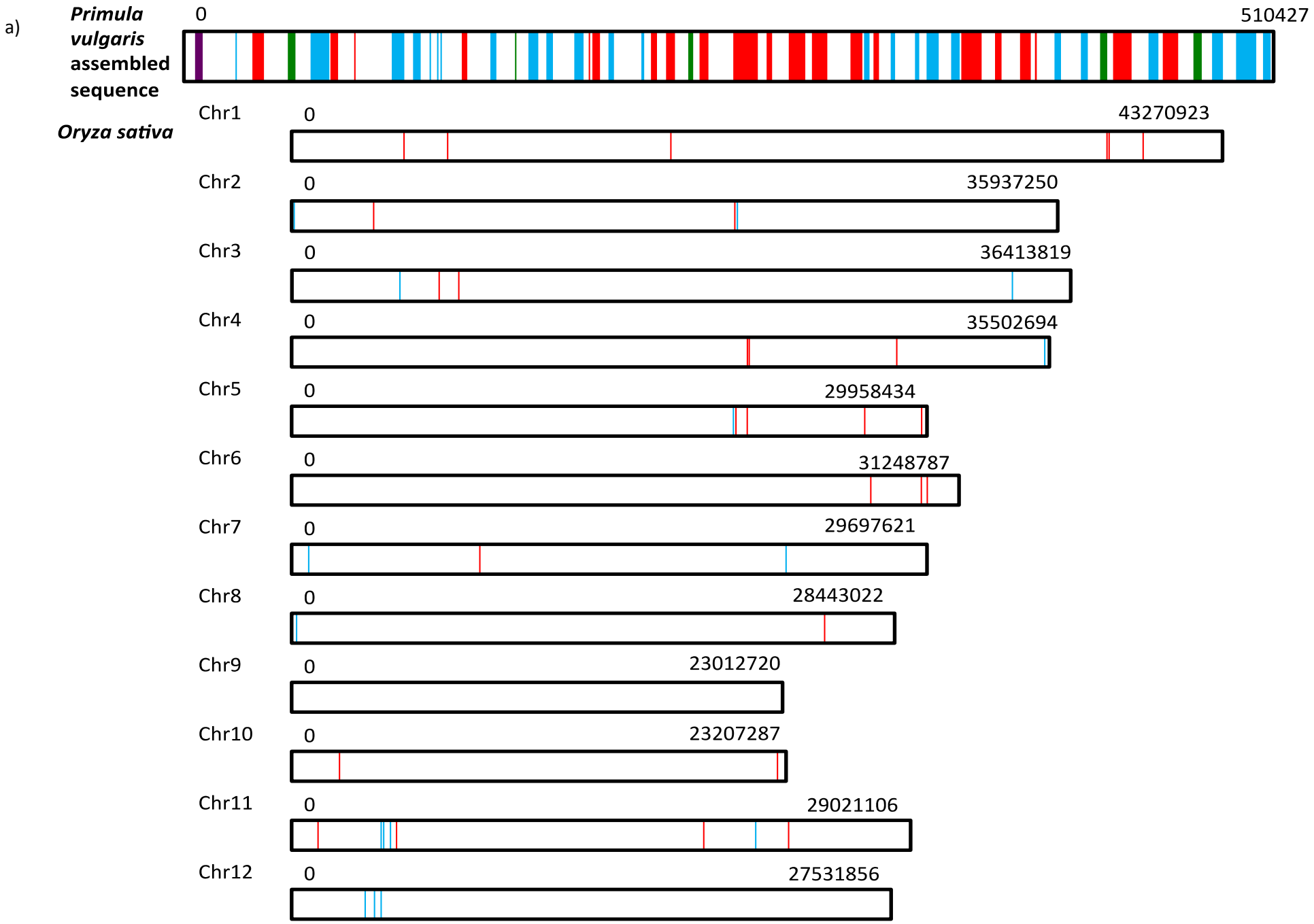


Figure 6.4: Locations of homologous genes in *M. truncatula.* Blue bars indicate genes in 5'-3' orientation and red indicates 3'-5'. a) The positions of homologous genes to those identified from the *Primula* contig in *Medicago truncatula.* Numbers denote number of base pairs in chromosomes. b) Lines link the genes from the *Primula* contig to their homologues in *Medicago*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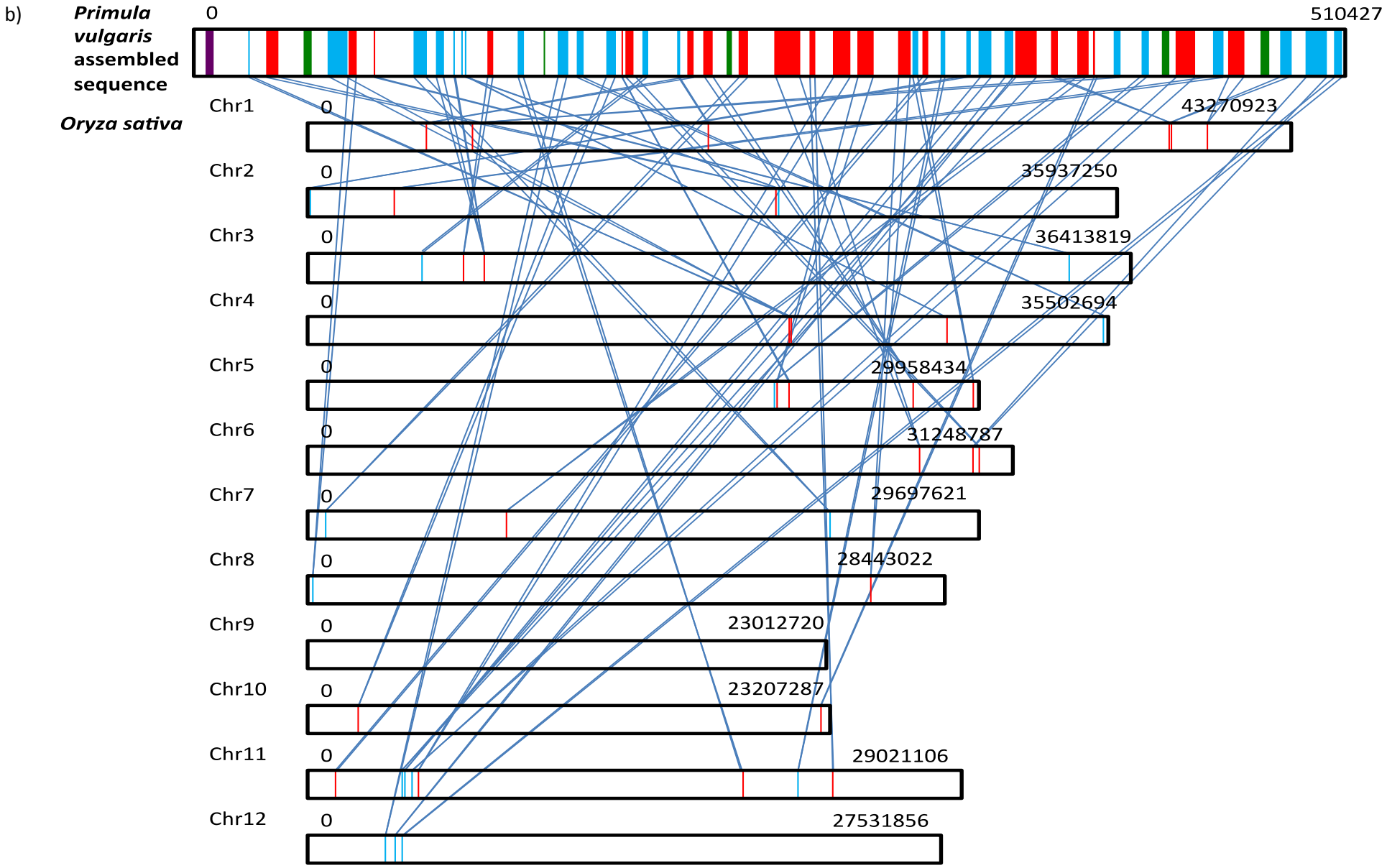


Figure 6.5: Locations of homologous genes in *O.sativa.* Blue bars indicate genes in 5'-3' orientation and red indicates 3'-5'. a) The positions of homologous genes to those identified from the *Primula* contig in *Oryza sativa.* Numbers denote number of base pairs in chromosomes. b) Lines link the genes from the *Primula* contig to their homologues in *Oryza.*

6.3 Discussion

6.3.1 Synteny between *P. vulgaris* and *A. thaliana*

Table 6.1 shows that all of the *Primula* queries used to search the TAIR database successfully identified homologues within *Arabidopsis*, with only four genes failing to find strong matches (*PvG25, PvG 31, PvG44* and *PvG48*). Interestingly, two of these four genes, *PvG25* and *PvG48,* identified the same gene within *Arabidopsis*, though closer inspection of the subject gene reveal that it encodes a retrotransposon polyprotein. One further gene of note is *PvG15*, a hypothetical protein predicted by the NCBI database, which identified a match from the *Arabidopsis* mitochondrial genome. Therefore, the presence of this gene within the assembled *Primula* contig suggests that it has transitioned between the chromosomes and the mitochondrial genome of either *Primula* or *Arabidopsis*, in one direction or the other.

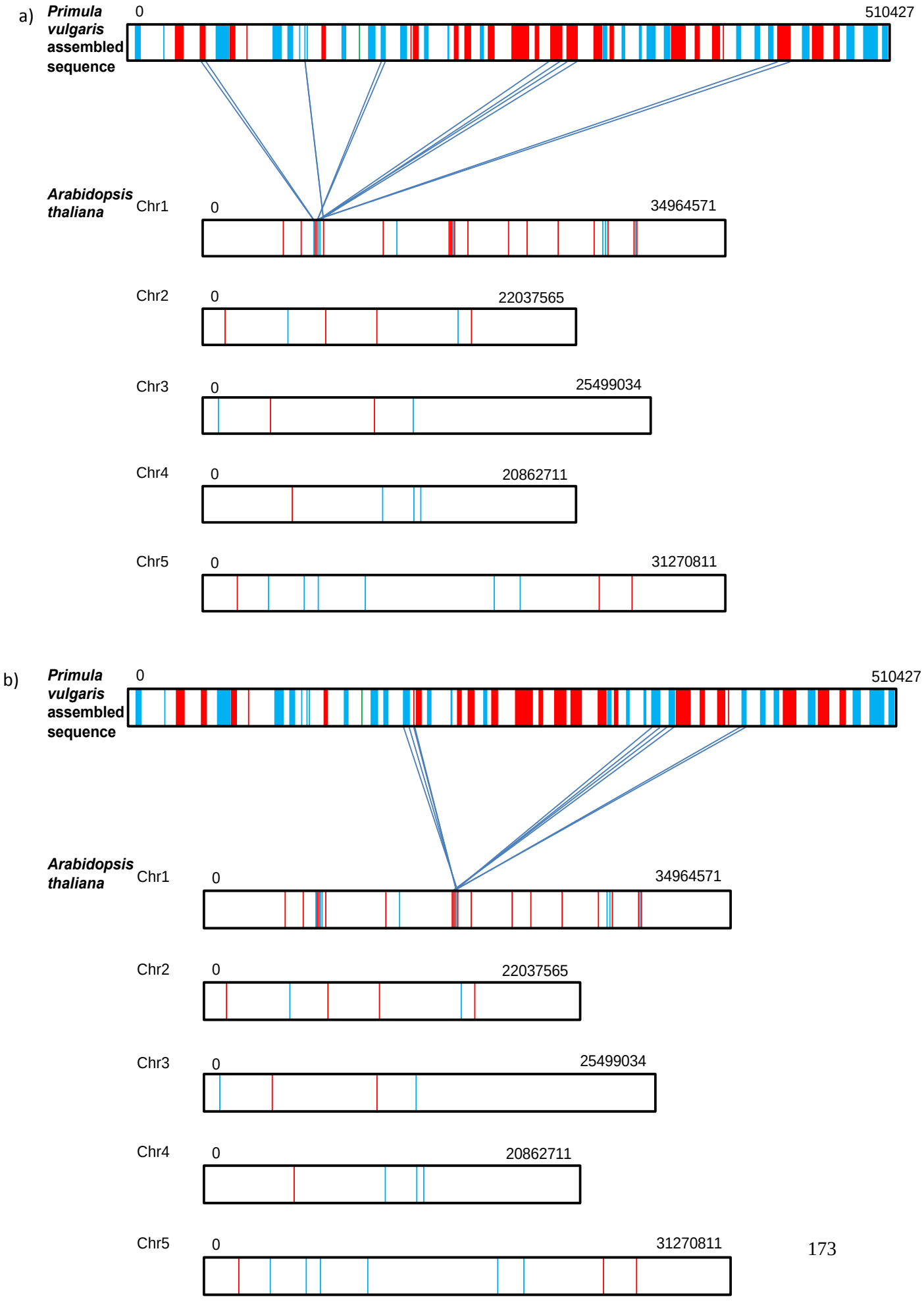
When identifying *Arabidopsis* homologues for those genes identified within the *Primula* contig, it was also possible to identify the location of these genes within the *Arabidopsis* genome, using the data shown in Table 6.1. Figure 6.2 shows the distribution of these genes throughout the *Arabidopsis* genome and it can be seen in Figure 6.2a) that, although the genes are spread throughout the five *Arabidopsis* chromosomes, there is a clear concentration of genes within Chromosome 1.

When the original *Primula* query genes are linked to their homologues, as in Figure 6.2b), another interesting result is highlighted. When taken in order from the 5' end of the *Primula* contig (from left to right), many genes do not, at first, show any particular degree of preservation in terms of gene order, with genes found next to each other in *Primula* located on different chromosomes in *Arabidopsis*. However, Figure 6.2b) shows that, across the assembled *P. vulgaris* sequence, there are a number of genes, that are close to each other in both species.

These groups of genes, found close together in both species, are shown more clearly in Figure 6.6. In this figure, it is possible to see clearly the clusters of genes located close to each other along *Arabidopsis* Chromosome 1 and the position of their *Primula* homologues along the assembled contig. Figure 6.6a) shows the first such cluster, containing 5 genes (*PvG4, PvG11, PvG17, PvG29, PvG30* and *PvG45*); the identities of which can be seen in Table 6.1. Most of these genes are not immediately next to each other along the *Primula* contig, however their close proximity to each other is still remarkable. In particular, *PvG29* and *PvG30,* found next to each other in *Primula* and within 700 bases of each other in *Arabidopsis.*

A similar cluster of genes can be seen in Figure 6.6b). In this example, *PvG18, PvG19, PvG36, PvG37* and *PvG42* are shown to be clustered together on *Arabidopsis* Chromosome 1. Similar to the cluster shown in Figure 6.6a), this cluster contains genes that are located directly next to each other in *Primula* though, in this example, there are two such pairs of genes; *PvG18 /19* and *PvG36/37.*

Figures 6.6c) and 6.6d) again show clusters of genes that are in close proximity to each other in both *Primula* and *Arabidopsis*, though in smaller numbers. Figure 6.6c) shows a cluster of three genes; *PvG2, PvG6* and *PvG39,* and Figure 6.6d) shows the three genes *PvG16, PvG38* and *PvG43* clustered together on Chromosome 1. Although none of the genes identified in these clustered are immediately adjacent to each other in *Primula*, it must be taken into consideration that the assembled contig represents a very small region relative to the entire *Primula* genome and, as such, these genes are still in close proximity to each other within the genome as a whole.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Arabidopsis thaliana
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Chr2
0
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Chr4
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Chr5
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31270811
b)
Primula vulgaris assembled sequence
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Arabidopsis thaliana
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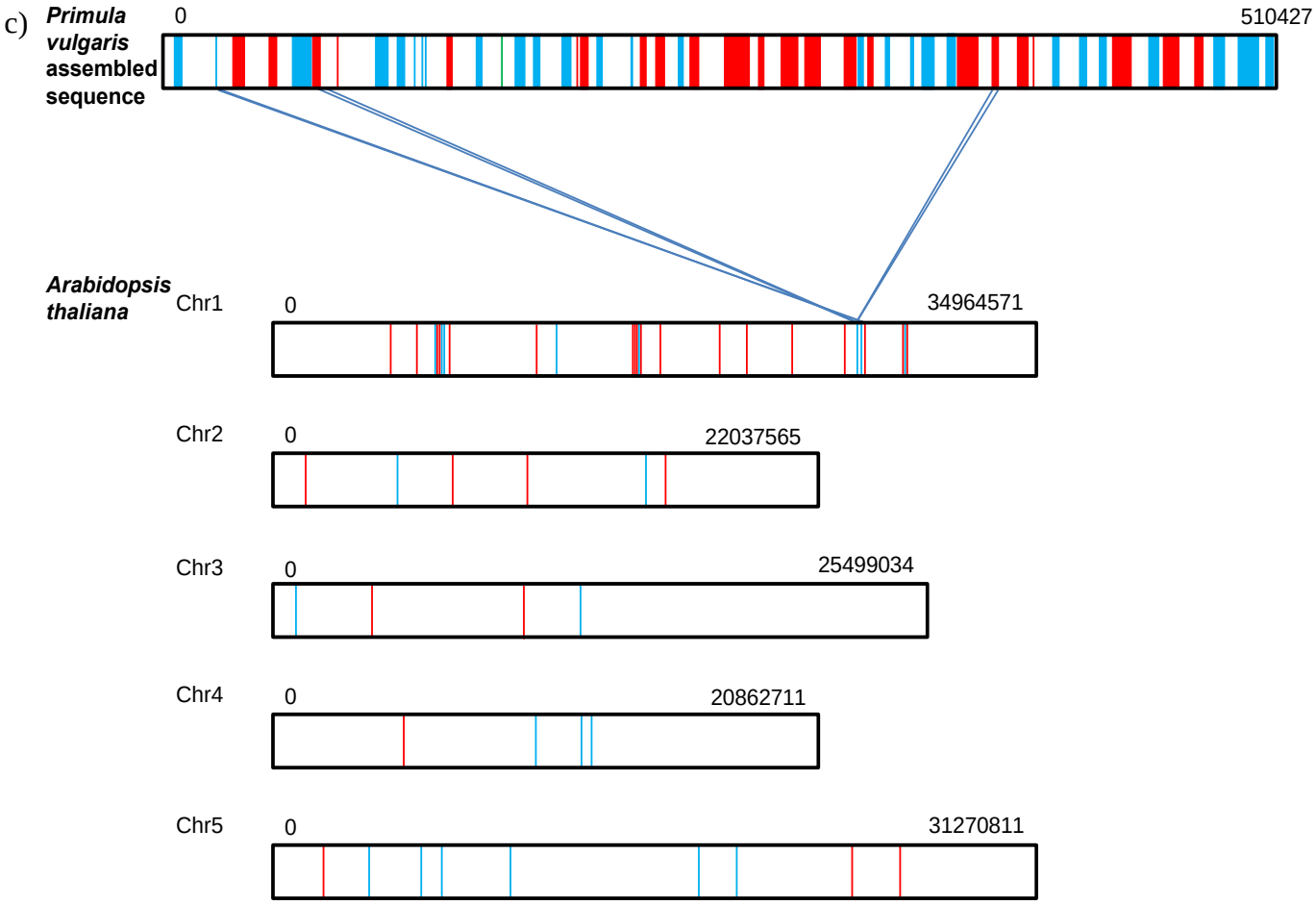


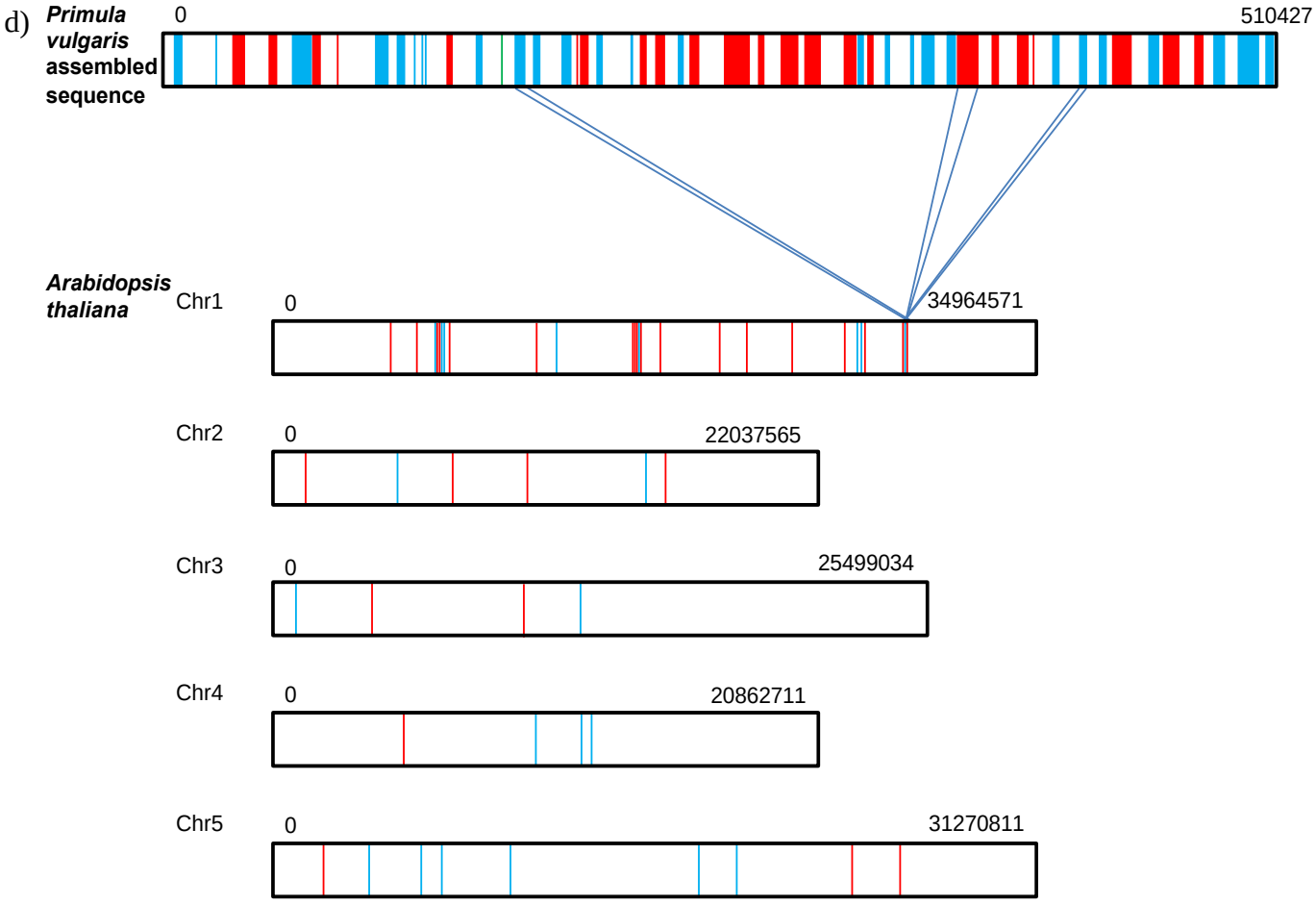


Figure 6.6: Positions of genes found in close proximity in both *P. vulgaris* and *A. thaliana*.. a) to d) show individual clusters of genes found together in both species.

Given the large divergence between the *Brassicaceae* and *Primulaceae*, it is intriguing to find that so many genes, taken from such a small sample of the *P. vulgaris*, genome can also be found so close together within the *Arabidopsis* genome. In particular, the presence of all of the gene clusters shown in Figure 6.6 within the same chromosome of *Arabidopsis* suggests a particular conservation of this specific region. Whilst the gene order may be significantly different in some areas, with a number of adjacent genes from *Primula* finding homologues on different chromosomes of *Arabidopsis*, there is clear evidence that specific lengths of sequence have been conserved by both species during evolution.

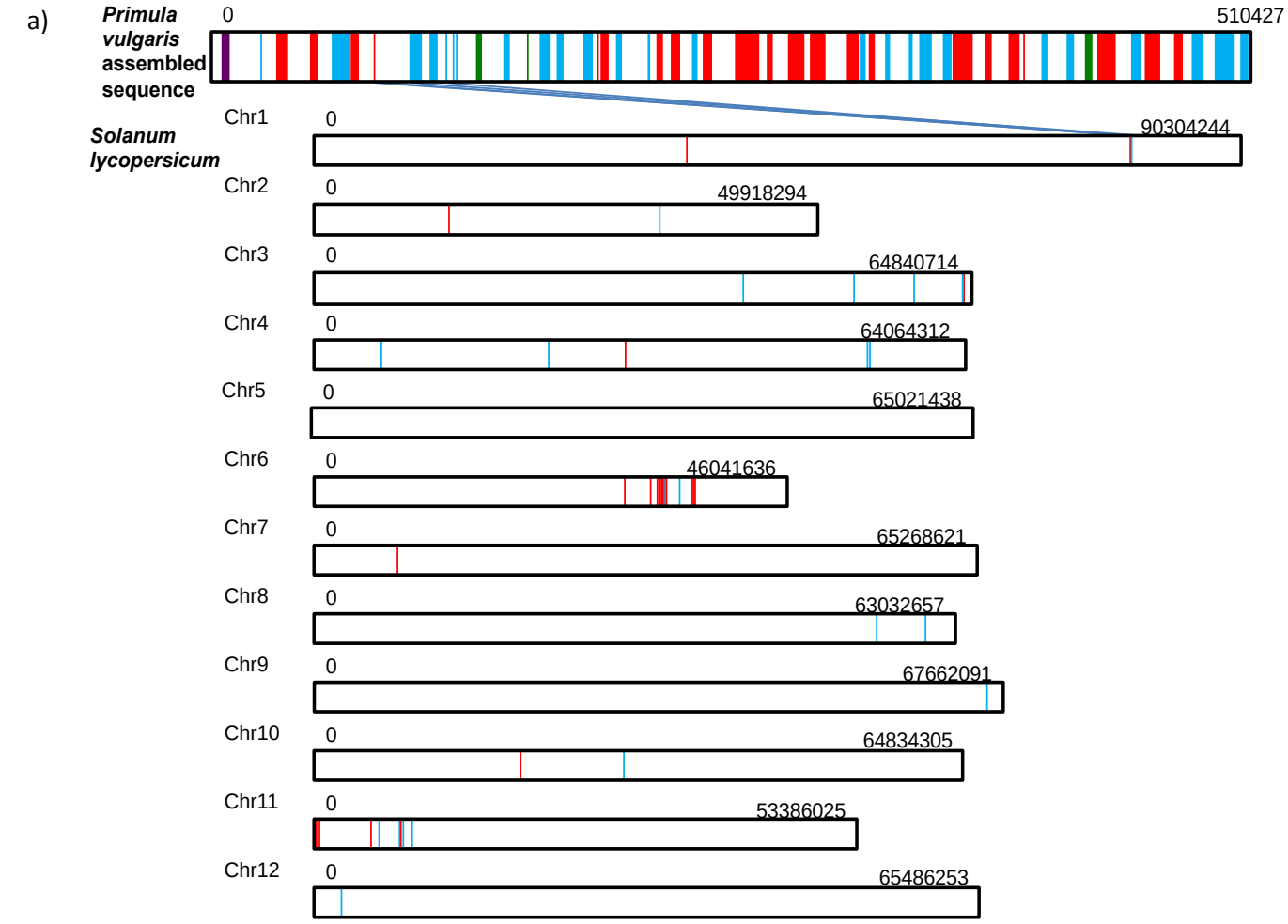
6.3.2 Synteny between *P. vulgaris* and *S. lycopersicum*

Table 6.2 shows that all but one of the *Primula* genes identified within the assembled contig were able to find homologues within the *S. lycopersicum* genome. The exception to this was *PvG1*, which encodes an ARS (autonomously replicating sequence) Binding Protein. Many of the subject genes identified in Table 6.2 also show strong levels of homology to the *Primula* queries used to search the Phytozome database. This is unsurprising, given the relative proximity of the two species within the phylogenetic tree of the Core Eudicots shown in Figure 6.1. However, in light of this, the absence of a *Solanum* form of *PvG1*, as determined by sequence homology, is perhaps significant. Tables 6.1 and 6.3 show that homologues of *PvG1* were identified in both *Arabidopsis* and *Medicago,* suggesting that it is a gene that has been lost by *Solanum*, and perhaps other *Solanaceae,* rather than one that has been gained by *Primula*. Another interesting result highlighted in Table 6.2 is that both *PvG7* and *PvG8* identified the same gene in the *S. lycopersicum* database. It is unknown whether this gene was duplicated within *Primula* or if one gene was lost

from *Solanum*, but both of these instances suggest a level of redundancy within the *Primula* genome.

Figure 6.3 uses the location data recorded in Table 6.2 to provide a graphic representation of the distribution of *PvG1-51* homologues throughout the *S. lycopersicum* genome. Similar to the pattern seen in *Arabidopsis*, Figure 6.3a) shows that the identified *Solanum* genes are found dispersed throughout the genome, though, in this instance, no homologue was identified on Chromosome 5. However, despite this spread, Figure 6.3a) also shows that the majority of the genes can be found very close to each other, with only a small number being found on their own. Whilst those on their own are spread out and dispersed across the chromosomes, many of the *Solanum* homologues identified are in tight clusters such as those seen on Chromosome 6 and Chromosome 11. Given the relatively small size of the *Primula* contig in comparison to the *Solanum* genome, this is already remarkable as it suggests that any redistribution of genes in the separate evolutions of the two species has preserved the same clusters of genes. Furthermore, Figure 6.3b), in which the identified homologues are shown in relation to the original *Primula* genes, shows that many of the same genes are found clustered together in both species.

The genes that have been found in close proximity to each other in both species are shown more clearly in Figure 6.7, which highlights the positions of these genes in both *Primula* and *Solanum.* In Figure 6.7a) to g), each of these groups of genes can be seen individually, and the positions of genes in both species can be seen.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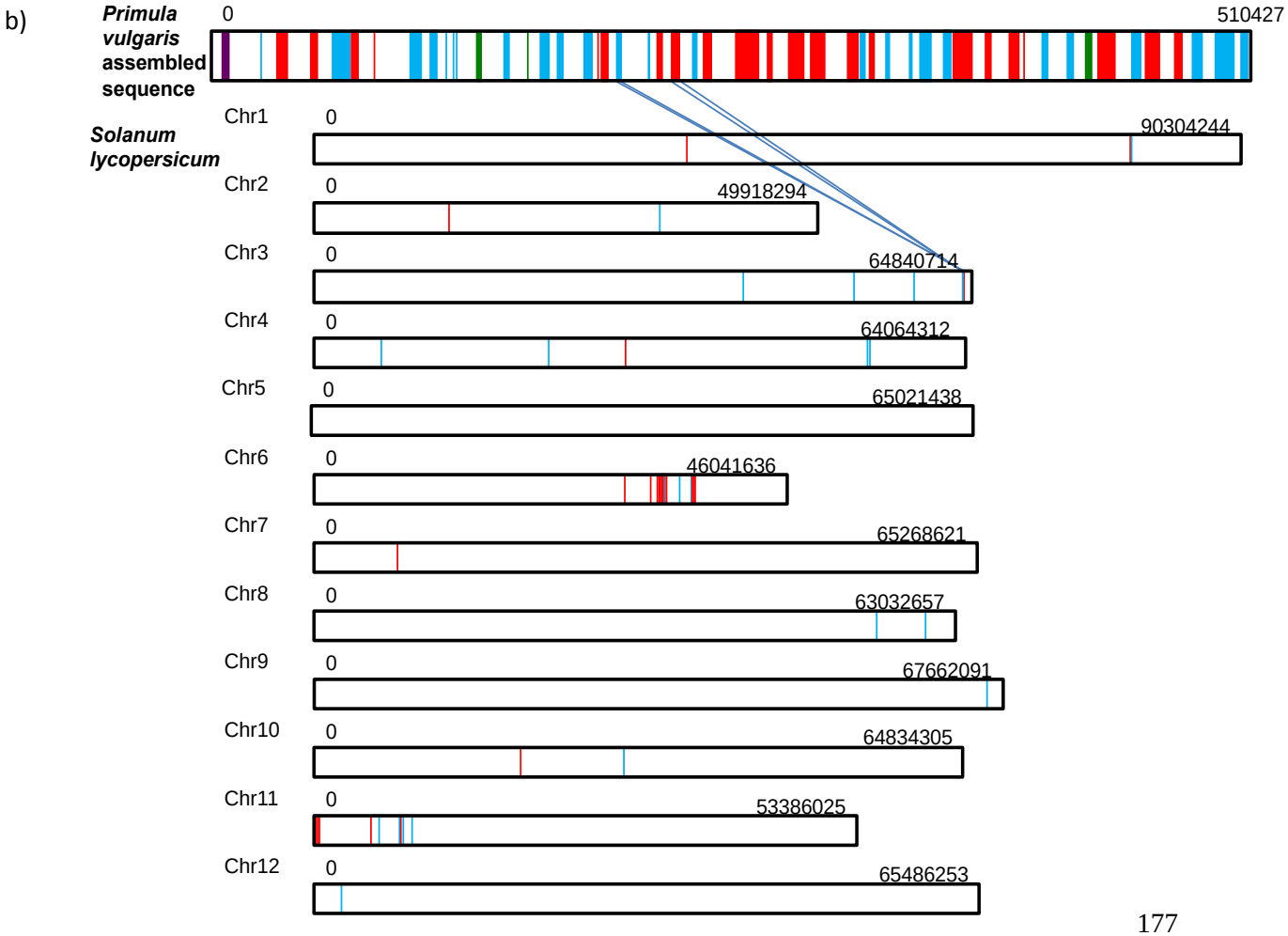
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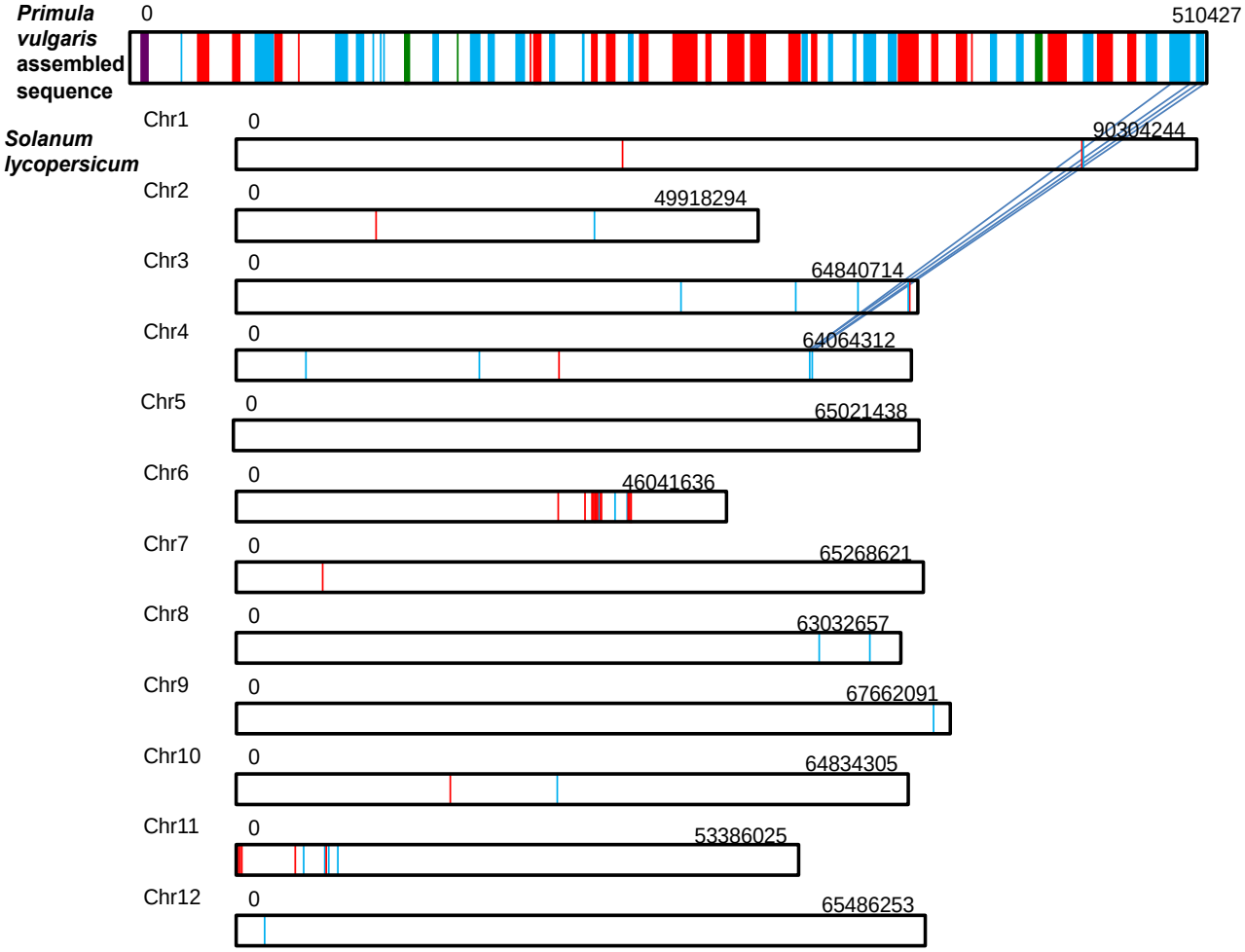
c)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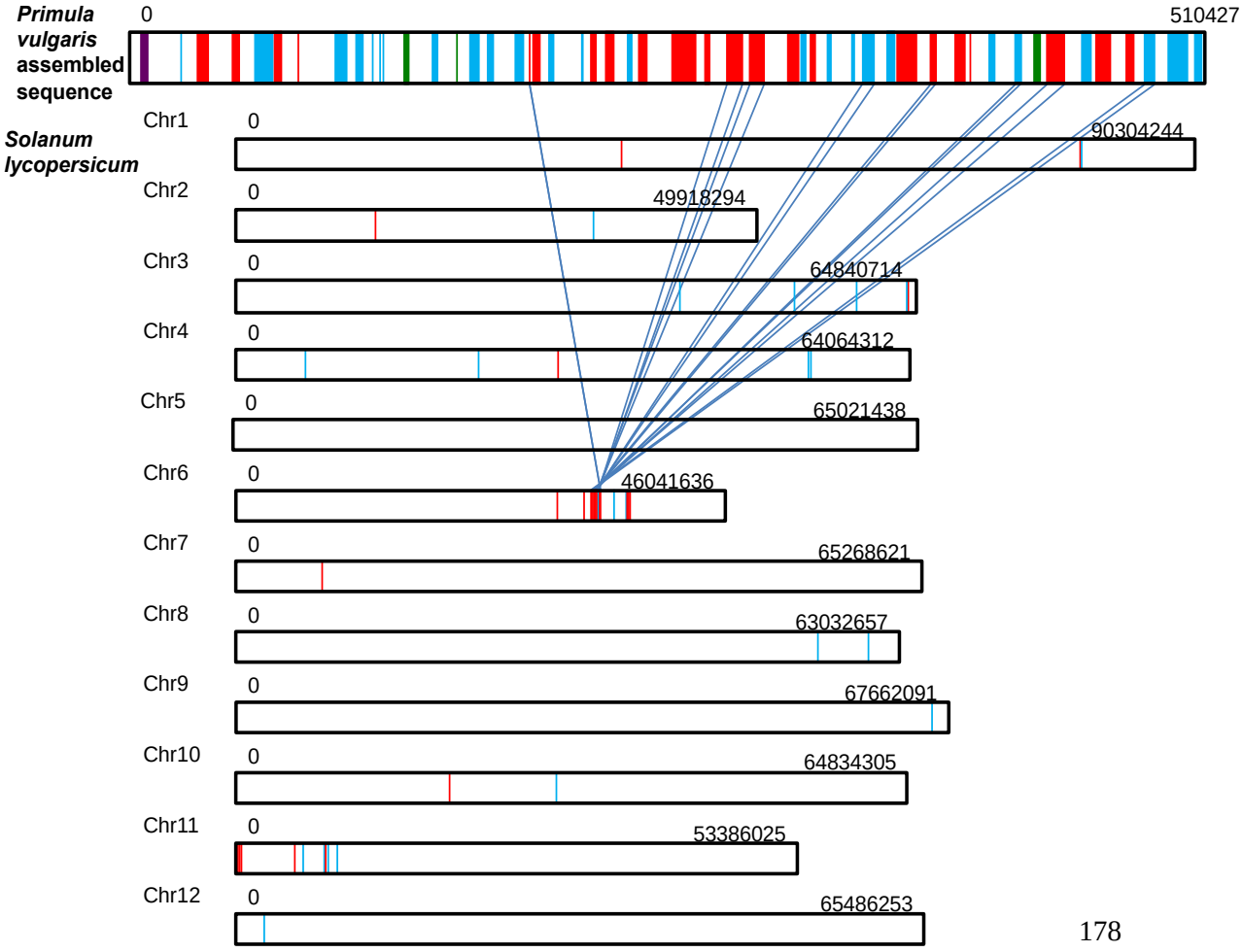
d)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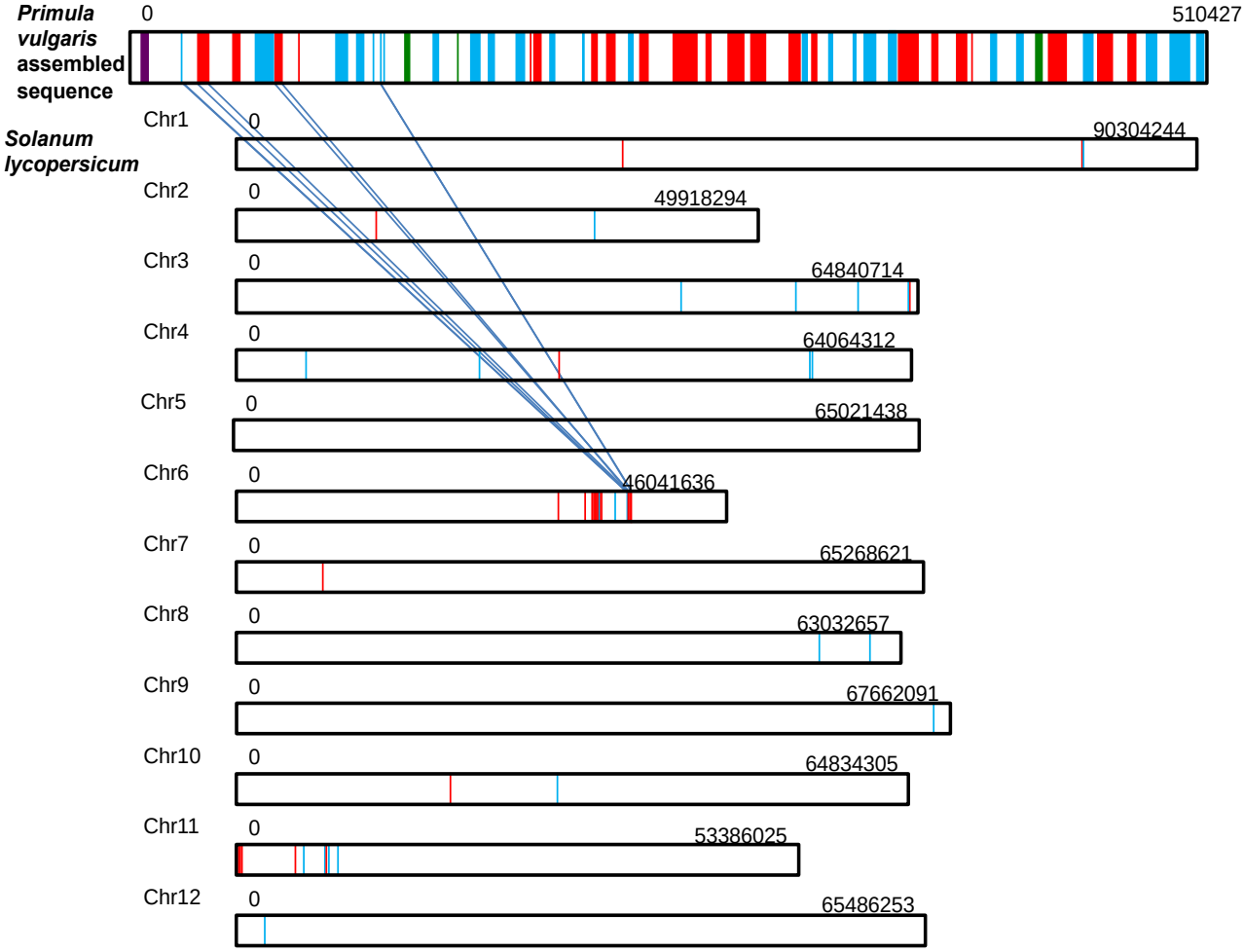
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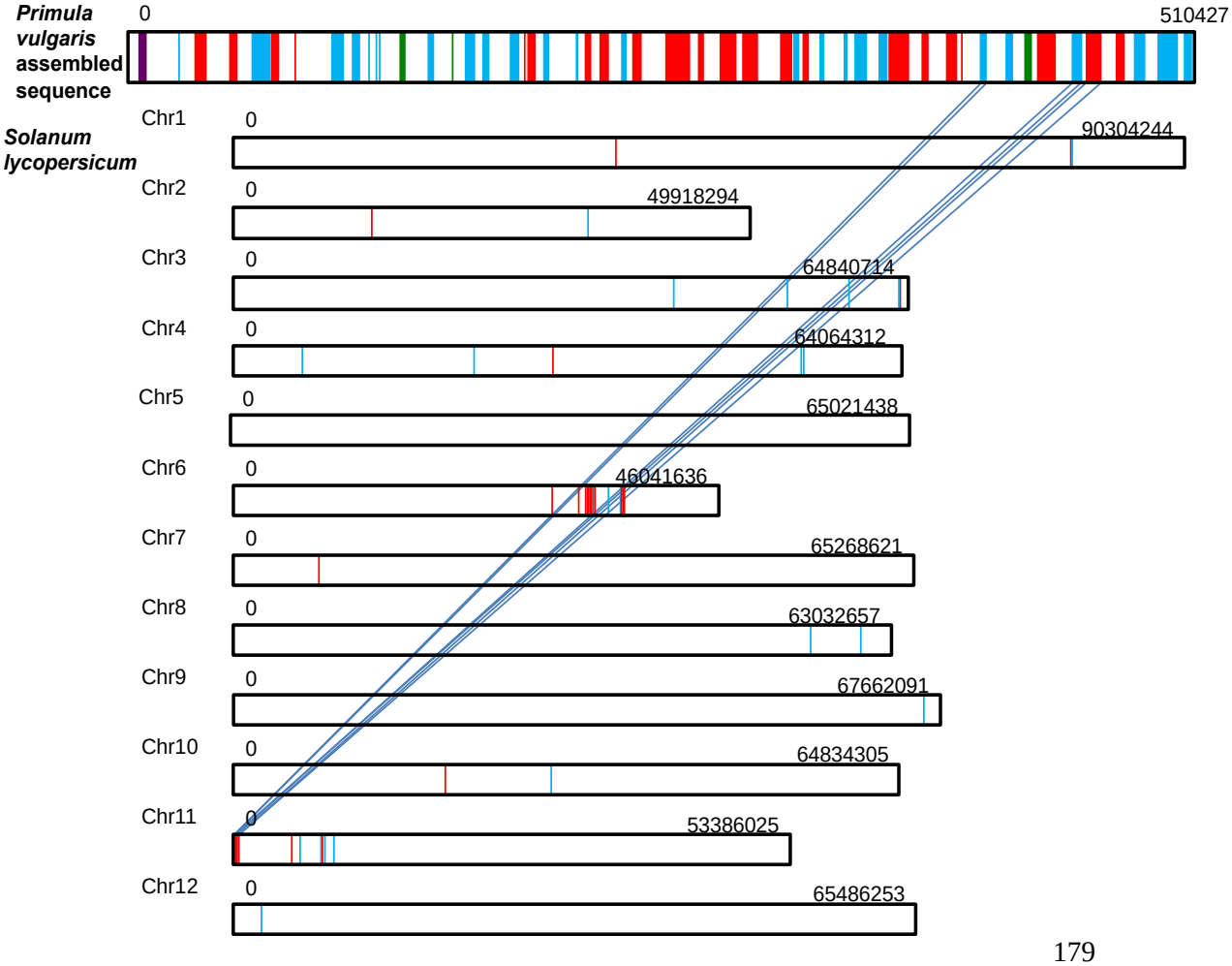
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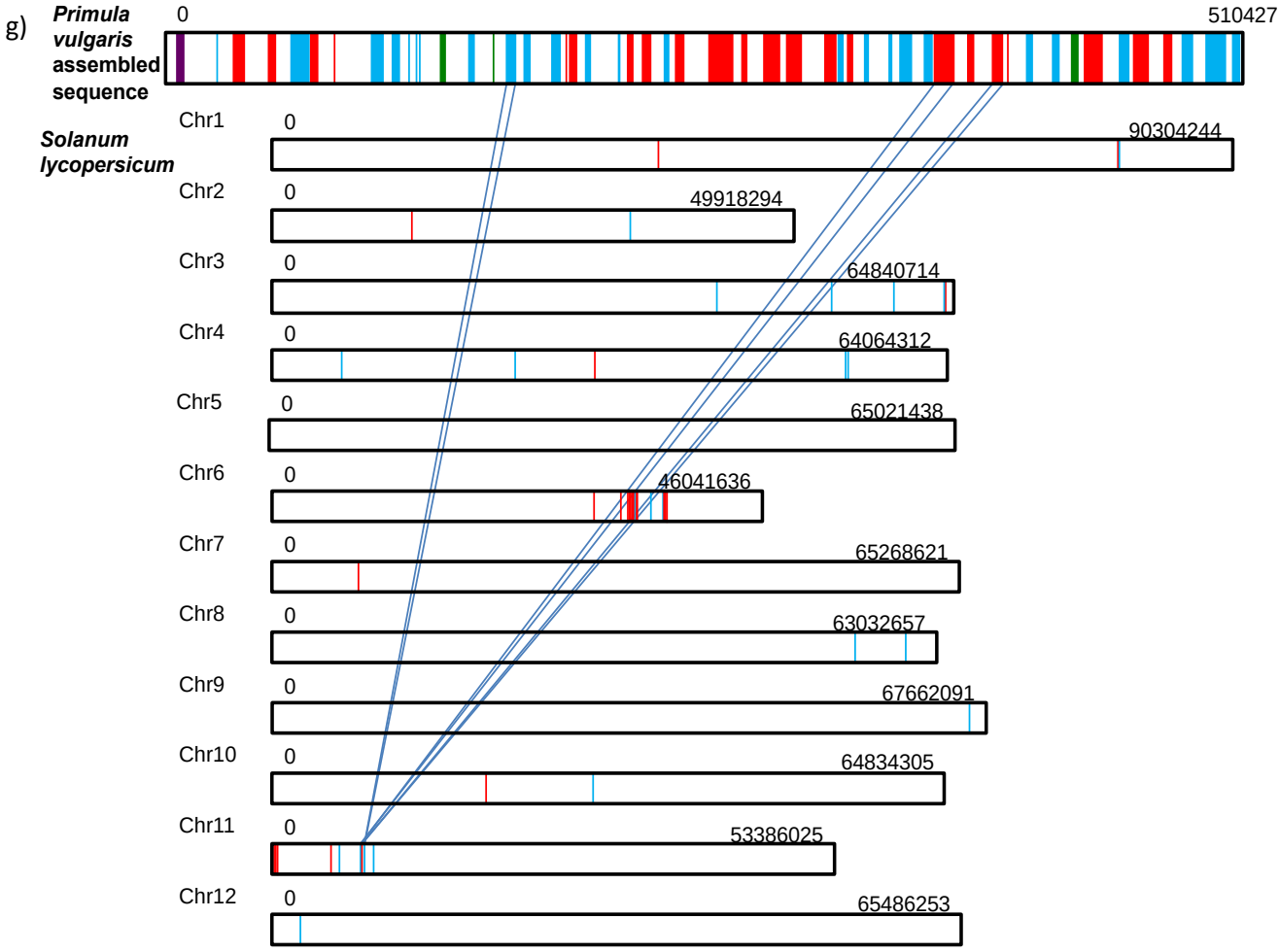


Figure 6.7: Positions of genes found in close proximity in both *P. vulgaris* and *S. lycopersicum*. a) to g) show individual clusters of genes found together in both species.

The first of these clusters is highlighted in Figure 6.7a), which shows the positions of homologues to *PvG7* and *PvG8*. These two genes, identified next to each other in *Primula* and separated by 17,177 bp are also found in Chromosome 1 of *Solanum*, 42 kb apart. This distance between the two genes in *Solanum* is significantly larger than that seen in *Primula* and the locus names of these genes, shown in Table 6.2, indicate that intervening genes can be found within this gap. As such, the smaller space between *PvG7* and *PvG8* in *Primula* suggests that these intervening genes have either been lost by *Primula* since the two species diverged. More likely explanations,

however, are that *Solanum* has either gained these extra genes in this time or that these intervening genes have moved into this region from elsewhere in the genome.

In contrast to this, Figure 6.7b) shows two genes found closer together in *Solanum* than in *Primula.* In *Primula*, *PvG21* and *PvG24* are over 23 kb apart whereas their *Solanum* homologues are within 20 kb of each other. Furthermore, the locus names of the corresponding *Solanum* genes indicate that a single gene lies between the two *Solanum* homologues. Again, this suggests that either *PvG22* or *PvG23* has been gained by *Primula* but not *Solanum*. However, since these two successfully identified homologues within *Solanum*, this would imply either a reshuffling of these genes during the evolution of the two species, or some level of redundancy.

Figure 6.7c) shows a similar scenario. In this figure, *PvG50* and *PvG51*, which are located within 4 kb of each other at the very end of the *Primula* contig, each identified homologues on Chromosome 4 of *Solanum*. Although the two *Solanum* homologues appear close to each other in Figure 6.7c), they are in fact over 239 kb apart. Again, this distance suggests an increase in the gap between these two genes and an increase in the number of genes within this region of the *Solanum* genome.

Figure 6.7d) shows the first of the larger clusters of genes identified, consisting of eight genes. The eight *Primula* genes identified in Figure 6.7d) (*PvG19, PvG29, PvG30, PvG36, PvG39, PvG43, PvG45* and *PvG49*) are relatively close to each other within the *Primula* contig and Table 6.2 shows that many of them are also extremely close together within Chromosome 6 of *Solanum*. For example, *PvG29* and *PvG30*, are within 3 kb of each other in *Primula* and within 1.5 kb of each other in *Solanum*, again providing evidence that gene order has been preserved between the two species.

Further evidence for the preservation of gene order is provided in Figure 6.7e), which shows *PvG2*, *PvG3*, *PvG6* and *PvG11*. Comparison between Figure 6.7d) and e) shows that this group of four genes (Figure 6.7e) is found in a similar position relative to the group of eight genes (Figure 6.7d) in both species. This, therefore, adds further support to the suggestion that this area has been conserved between the two species, even if the intervening genes between these two groups have either been lost or moved.

The identification of two clusters of genes with a preserved gap between them in both species suggests an importance of both the clusters and the gap itself. It also poses not just the question of why these genes were conserved, but also why those genes between them were either lost or allowed to disperse within the genome. Similarly, it is unknown whether the two clusters were preserved separately or whether the region between them was also preserved at first but lost later.

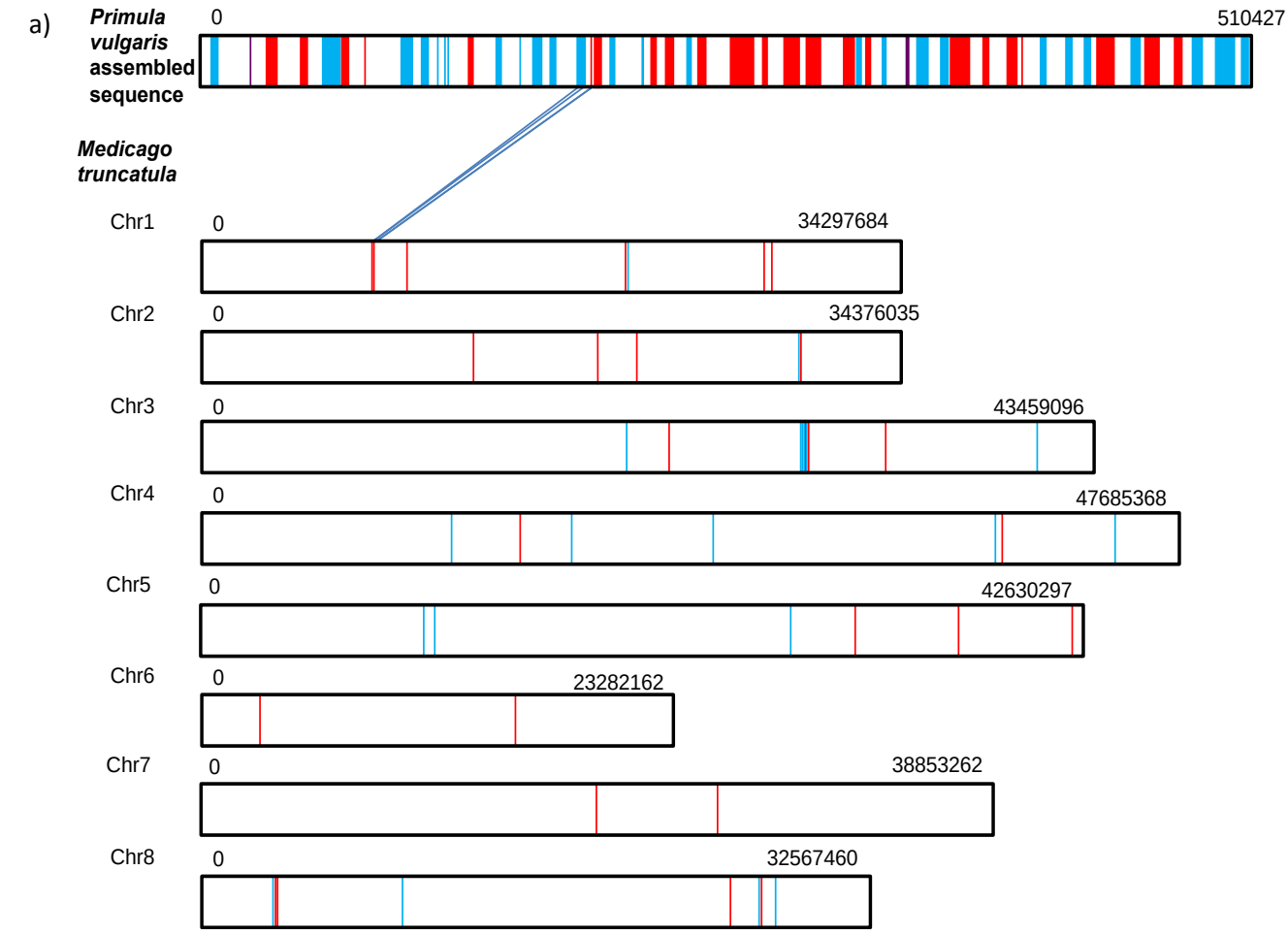
Figure 6.7f) and g) show a similar occurrence with homologues identified on Chromosome 11 of *Solanum*. In Figure 6.7f) *PvG42*, *PvG46* and *PvG47* are shown to have homologues clustered at the very start of Chromosome 11. Although *PvG42* lies slightly further from *PvG46*, Table 6.2 shows that *PvG46* and *PvG47* are 1964 bp apart in *Primula* and 2123 bp apart in *Solanum*, a difference of just 159 bp. Similarly, Figure 6.7g) shows a cluster of genes further along Chromosome 11 identified as homologues of the *Primula* genes *PvG16*, *PvG38* and *PvG40*. Though these are not as closely positioned within the two contig as *PvG46* and *PvG47*, the preservation of this gene cluster may still be seen as significant, particularly if viewed in conjunction with Figure 6.7f). Within the *Primula* contig, *PvG16* remains isolated from the other genes highlighted in these two figures, whereas *PvG38*, *PvG40*, *PvG42*, *PvG46* and *PvG47* are all positioned relatively near to each other,

with 85 kb between *PvG38* and *PvG47*. In contrast to this, over 8 mb lie between the homologues of these same two genes in *Solanum*. This suggests that the regions between these two groups of preserved genes have been lost. Additionally, when these results are compared with those shown in Figure 6.7d), it can be seen that the areas directly surrounding these genes has not been similarly conserved. For example, whilst *PvG38* and *PvG40* as well as *PvG46* and *PvG47* appear to show conservation between the two species, those genes around them such as *PvG36*, *PvG43* and *PvG45* appear to have been preserved separately, with homologues on chromosome 6 rather than chromosome 11. This observation raises questions about the manner in which these particular genes were preserved as the two species diverged. A number of pairs of genes have been preserved between the two species but they are mixed with other groups that have been preserved separately. As a result, it is unknown whether these genes originated on separate chromosomes before being condensed to a region near to each other in *Primula* or if, in fact, they have been dispersed within the *Solanum* genome as the species have evolved.

The synteny observed between *Primula* and *Solanum* is significant as it demonstrates that the gene order observed in the assembled *P. vulgaris* contig has changed little since the species diverged from its common ancestor with *Solanum*. As discussed in 6.1, this provides strong evidence to suggest that the genes in this region were already present before the key *S* locus genes converged within this area of the genome. Furthermore, the conserved gene order seen between *Primula* and *Solanum* provides extra evidence that the assembly of the *P. vulgaris* contig, as described in Chapter 4, is correct.

6.3.3 Synteny between *P. vulgaris* and *M. truncatula*

Following the annotation of the genes identified within the assembled *Primula vulgaris* contig, homologous genes from *Medicago truncatula* were identified using the translated nucleotide sequences of the *Primula* genes as queries in BLASTP searches of the Phytozome database. The results of these searches, shown in Table 6.3, show that the majority of *Primula* queries were able to identify homologues in *Medicago*, the only exception being *PvG2*. However, the absence of *PvG2* within the *Medicago* genome is unsurprising given its identity as *SLL1*, a gene known to be tightly linked to the *Primula vulgaris S*-locus. With this exception, the results shown in Table 6.3 serve to demonstrate a high level of preservation of sequence homology between the two species. Also worthy of note are *PvG9* and *PvG10*. As seen in *S. lycopersicum*, these two *Cytochrome P450* genes identified the same homologue within *Medicago truncatula* though, as discussed in 6.3.2, the reason for is unknown. The data recorded in Table 6.3 is also represented graphically in Figure 6.4, which shows the distribution of the identified homologues throughout the *M. truncatula* genome. Figure 6.4a) shows that many of the homologues of *PvG1-51* are dispersed widely throughout all eight *M. truncatula* chromosomes. This is a contrast to the results discussed in 6.3.1 and 6.3.2, in which clear concentrations of genes have been observed within one or two chromosomes. However, some clusters of genes, similar to those seen in Figure 6.2 and Figure 6.3, do exist and Figure 6.4b), in which the *Medicago* homologues are shown relative to the original *Primula* query genes, shows these. Figure 6.8 shows each of these clusters more clearly.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Medicago truncatula
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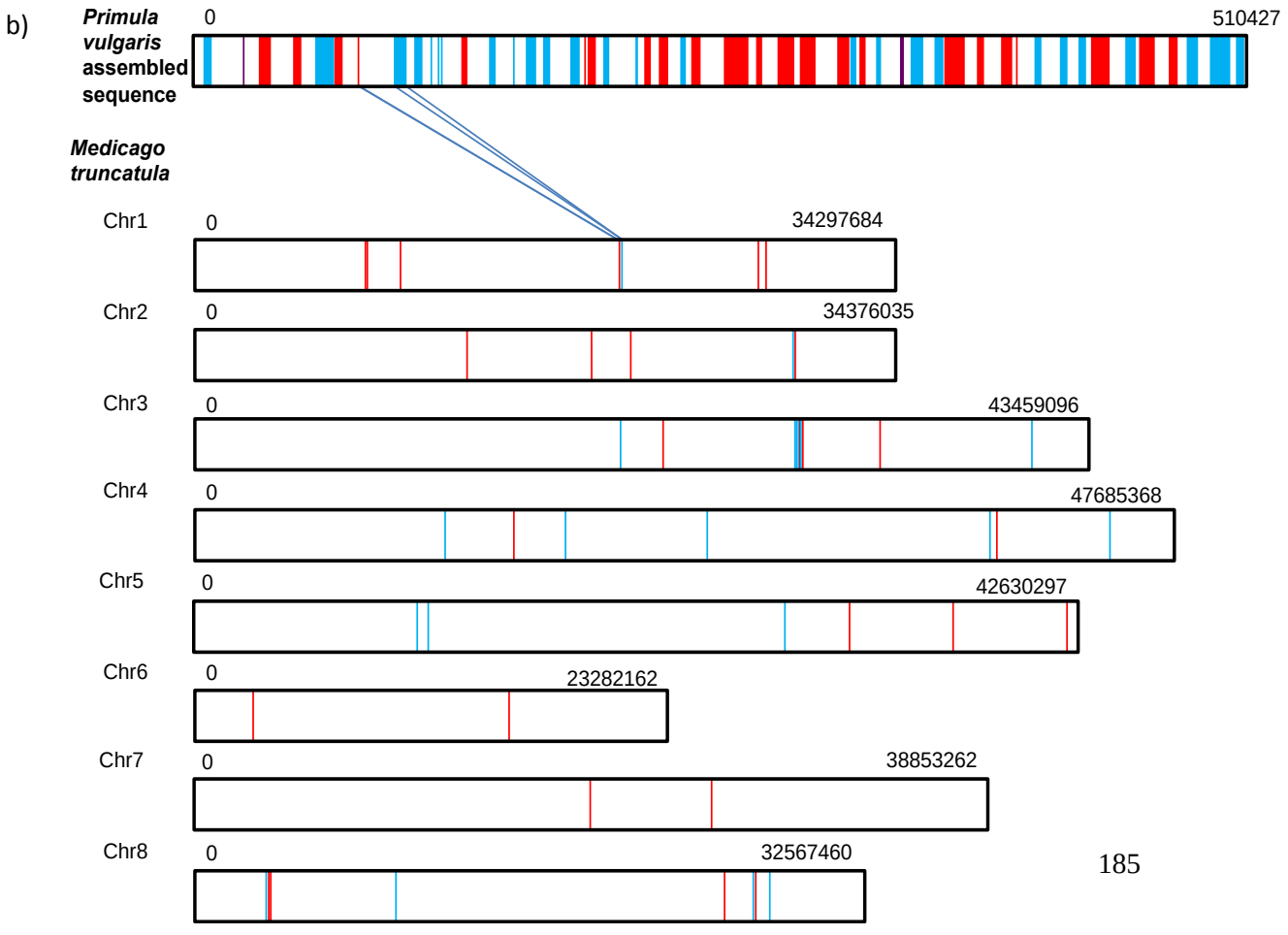
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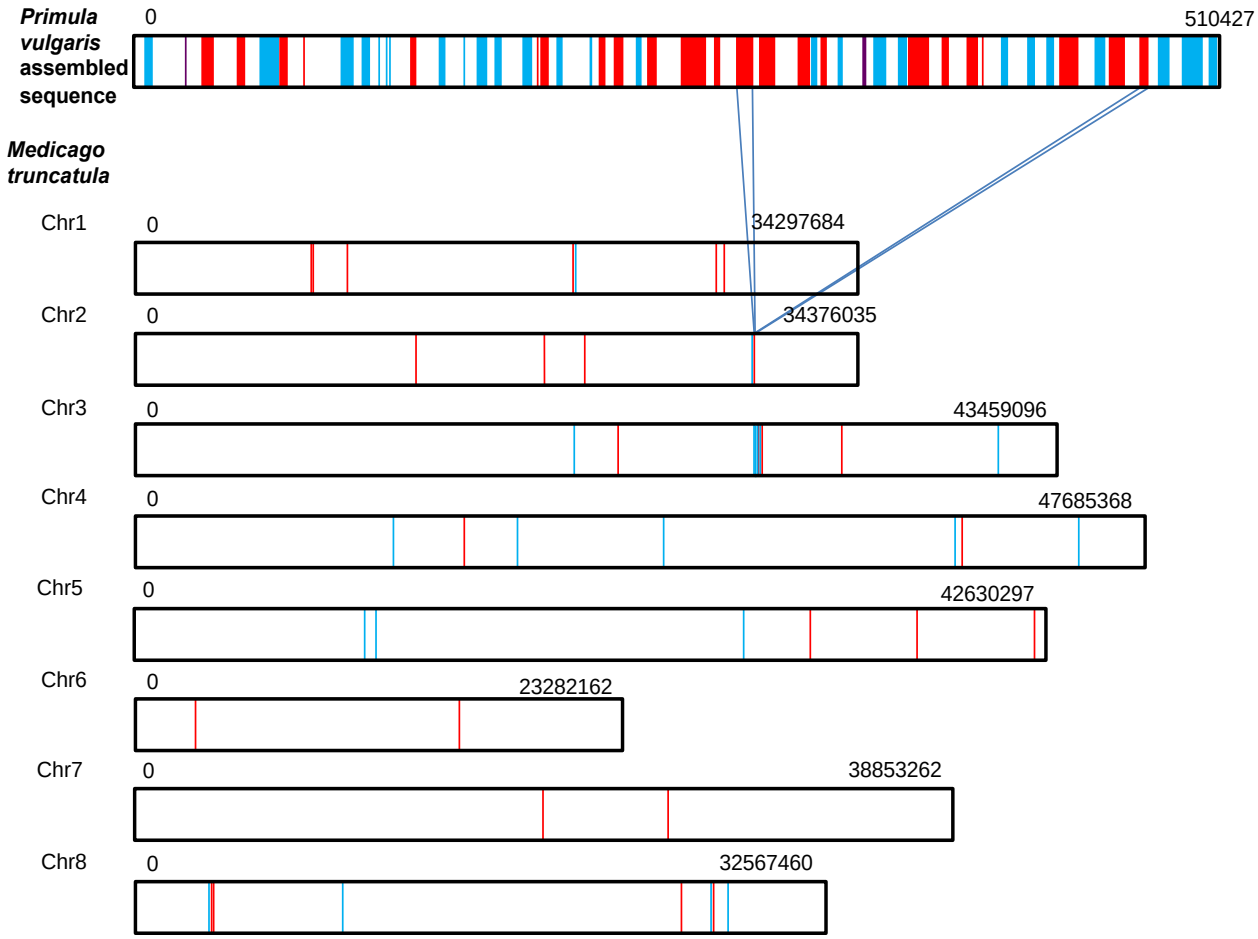
c)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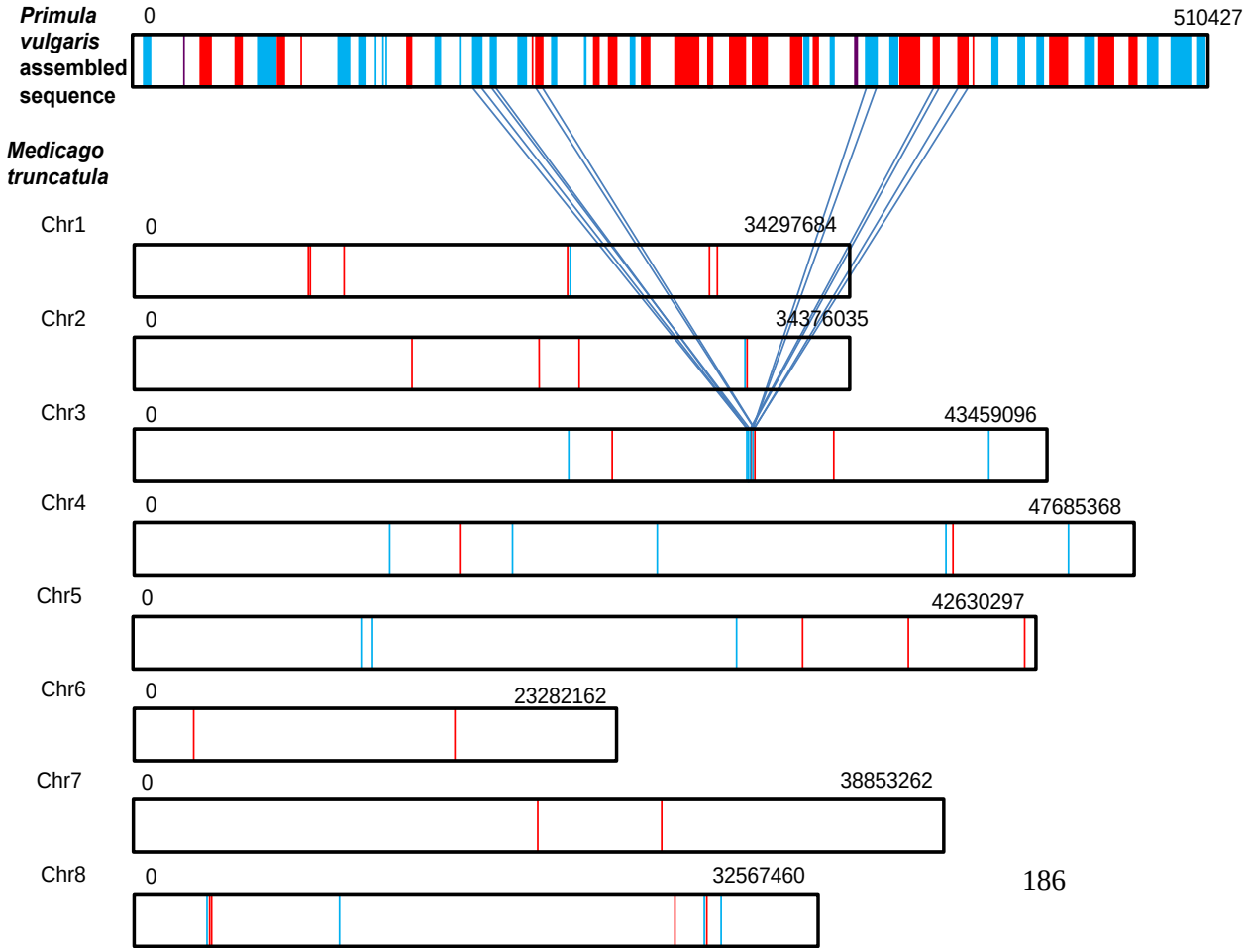
d)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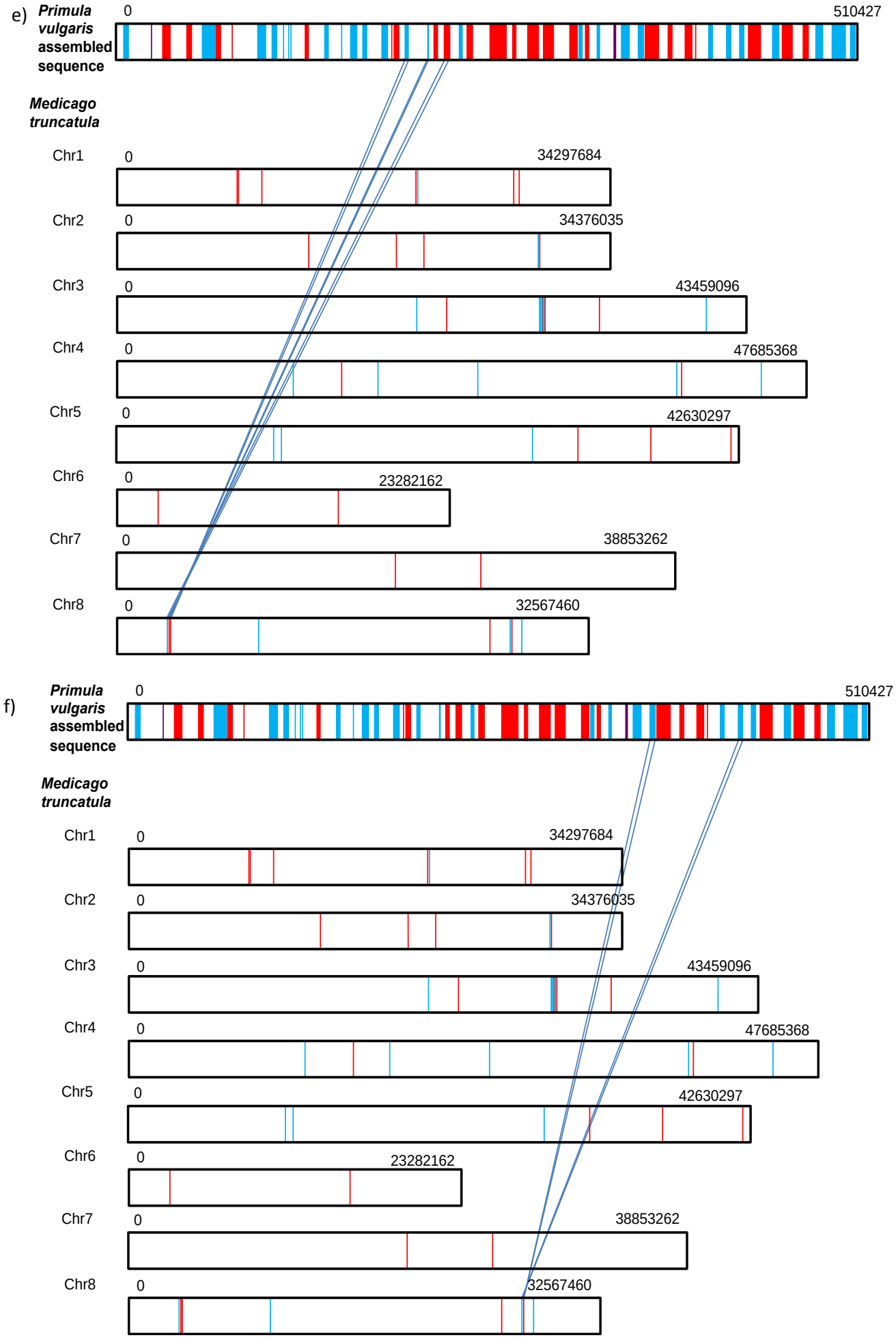

Figure 6.8: Positions of genes found in close proximity in both *P. vulgaris* and *M. truncatula*. a) to f) show individual clusters of genes found together in both species.

The first of these clusters is shown in Figure 6.8a) *PvG18* and *PvG19*. These two genes, found under 800 bp apart in *Primula* mapped to homologues in *Medicago* over 17.5 kb apart, the locus names of each gene suggests that there are others between the two *Medicago* genes. As discussed for similar instances in *S. lycopersicum* in 6.3.2, the absence of these genes within the *Primula* contig suggests that they may have been lost from this region of the genome or gained by the other in the time since the two species diverged.

Figure 6.8b) shows a similar occurrence, with two genes in close proximity on Chromosome 1 of *Medicago* displaying homology to two genes located next to each other in *Primula.* As in the case described above, these two genes are just over 17 kb apart in *Primula* whereas their homologues are over twice as far apart (36.2 kb) in *Medicago*. Further to this, the Locus Names of the two *Medicago* genes also suggest that more genes can be found between these two genes in this species that are not present within the *Primula* contig.

The pair of genes shown in Figure 6.8c) represents a different pattern to those already described. In Figure 6.8c), *PvG29* and *PvG48*, two genes over 182 kb apart in *Primula,* are shown to have homologues in *Medicago* that are under 49 kb apart. This pattern of distribution is directly opposite to those genes highlighted in Figures 6.8a) and b) in the *Medicago* homologues are further apart than the original *Primula* queries. As in similar examples discussed already, it is difficult to tell whether these two genes have diverged within *Primula*, or have converged in *Medicago*. However, it is clear that they have not been preserved between the two species to the same extent as those shown elsewhere in Figure 6.8. Despite this, it cannot be said that they have not been subject to some level of conservation. Although the two *Primula* genes appear relatively distant within the assembled *Primula* contig in the figure, the

scale of the Figure 6.8 must be considered, especially in relation to the size of the *Medicago* chromosomes shown. Therefore, within the *Primula* genome, *PvG29* and *PvG48* can still be considered close neighbours.

Figure 6.8d) shows the largest of the gene clusters identified for *M. truncatula.* Interestingly, this figure shows that the original six *Primula* genes used to identify those in *Medicago* are found in two groups of three genes, with the first (*PvG16, PvG17* and *PvG20*) over 15.4 kb apart from the second group (*PvG36, PvG39* and *PvG40*). The gap between these two groups of *Primula* genes raises the same questions discussed above for Figure 6.8c), and it remains unclear whether the two groups have been separated in *Primula* or have converged in *Medicago*. Further inspection of Figure 6.8d) also shows that the *Medicago* homologues do not show the same order as the original *Primula* query genes. Whilst PG16 and *PvG17* are found next to each other in *Primula* and very close together in *Medicago*, the genes shown adjacent to *PvG17* in the Figure 6.8d) is *PvG40,* with the *Medicago* form of *PvG20* at the 3' end of the cluster. This change in order suggest that, although the genes have stayed in close proximity to each other in both species, certain pairs of genes within the group have been allowed some level of movement. Particular examples of these are *PvG16* and *PvG17*, which have remained within 7.5 kb of each other in both species. Other interesting examples are *PvG36* and *PvG39*, found almost 30 kb apart in *Primula*, but identified within 14 kb of each other in *Medicago*. Furthermore, the order of these two genes has also been reversed between the two species.

PvG39 and *PvG40* have displayed the opposite action to that between *PvG36* and *PvG39*, showing an increased distance between the two genes in *Medicago* compared to *Primula*. However, among the genes in Figure 6.8d), it is the movement of *PvG20* relative to the others that is perhaps most interesting and it is unclear why this particular gene has changed its position within the order of the genes to the extent that it has.

Figure 6.8e) shows the positions of three more genes (*PvG21*, *PvG22* and *PvG24*) that are found in close proximity in both species, with 23,658 bp separating the three genes in *Primula* and 41,628 bp separating them in *Medicago*. Although these three genes were identified on Chromosome 8 of *Medicago*, the closest homologue of *PvG23*, found among these genes in *Primula*, was found on Chromosome 4. Again, it is unclear whether this gene was separated from the others as *M. truncatula* evolved or if it converged with *PvG21*, *PvG22* and *PvG24* in the evolution of *P. vulgaris*. However, the point of note for this cluster, as well as for that shown in Figure 6.8f), is that the order of the genes has been reversed between the two species. In Figure 6.8f), *PvG37* and *PvG43* are shown in relation to their *Medicago* homologues, identified on Chromosome 8, with the two genes found in the opposite order when the chromosome is read in the same direction as the assembled *Primula* sequence. The reason for this change in order is unclear, though the discovery of both clusters in Figure 6.8e) and f), suggests that the genes have been preserved as a group, even if the order of the genes within the group has been lost.

6.3.4 Synteny between *P. vulgaris* and *O. sativa*

Similar to the results shown in Table 6.2, Table 6.4 shows that the majority of *Primula* query genes were able to identify homologues within *O. sativa*, with the sole exception of *PvG1*. The repeated absence of this gene is interesting, though the reason that a homologue could not be identified in either *S. lycopersicum* or *O. sativa* remains unknown. The discovery of a gene that is present in one species but not the other is not unexpected, given the large divergence between the two species within the plant kingdom. However this correlation between *Solanum* and *Oryza* is itself surprising, given that a homologue of *PvG1* was identified in both *Arabidopsis* and *Medicago*, neither of which are particularly close relatives of *Primula*. Table 6.4 also shows that a number of *Primula* queries identified homologues outside of the 12 main chromosomes of *Oryza*. These five genes, *PvG4*, *PvG15*, *PvG25*, *PvG44* and *PvG48* mapped to either an unanchored pseudomolecule used to represent unanchored BAC clones (ChrUn) or another pseudomolecule representing unmapped Syngenta sequences (ChrSy), as used by the Rice Genome Annotation Project (Ouyang *et al.*, 2007). Of these five genes, the homologues of *PvG4*, *PvG44* and *PvG48* mapped to ChrUn while *PvG15* and PvG25 mapped to ChrSy.

As seen in *M. truncatula* and *S. lycopersicum*, Table 6.4 shows that *PvG9* and *PvG10*, two *Cytochrome P450* genes, identified the same subject *in O. sativa*. As discussed in 6.3.2, the source of this apparent redundancy within the *Primula* genome is unclear, and it is unknown whether it is the result of a duplication of the gene within *Primula* or a loss of the gene within *Oryza*.

With the exception of *PvG1*, the results presented in Table 6.4 show that there has been a high level of sequence homology between *Primula* and *Oryza*, despite the distant relationship between the two species.

Figure 6.5 shows the distribution of the genes and homologues described in Table 6.4 throughout the assembled *Primula vulgaris* contig and the 12 *Oryza sativa* chromosomes. As can be seen clearly in Figure 6.5a), homologues were identified on 11 of the 12 *Oryza* chromosomes, with Chromosome 9 the only example on which no homologues were identified. The figure also shows that many of the homologues are relatively isolated, with large physical distances between the next highlighted gene. Although there are some instances of genes near to each other, these are often found with only one other gene nearby. This wide spread of genes throughout the genome serves to emphasise examples, such as on Chromosome 11, where genes have been identified close together, suggesting that some level of conservation in gene order has still occurred.

Figure 6.5b) shows the relationship between the genes identified in *Oryza* and the *Primula* genes used to identify them, with lines linking homologous genes together. Homologues within the ChrUn and ChrSy pseudomolecules are not shown. With the these five genes and *PvG1* (discussed above) excluded, Figure 6.5b) shows that no genes found immediately next to each other in *Primula* can also be found next to each other in *Oryza*. Interestingly, however, many genes found in close proximity to each other in *Primula* identified homologues on separate chromosomes of *Oryza*, demonstrating that the conservation of gene order between species it is not in fact as high as suggested by Figure 6.5a).

As discussed above, a number of genes were observed near to each other in both species, and these are shown more clearly in Figure 6.9.

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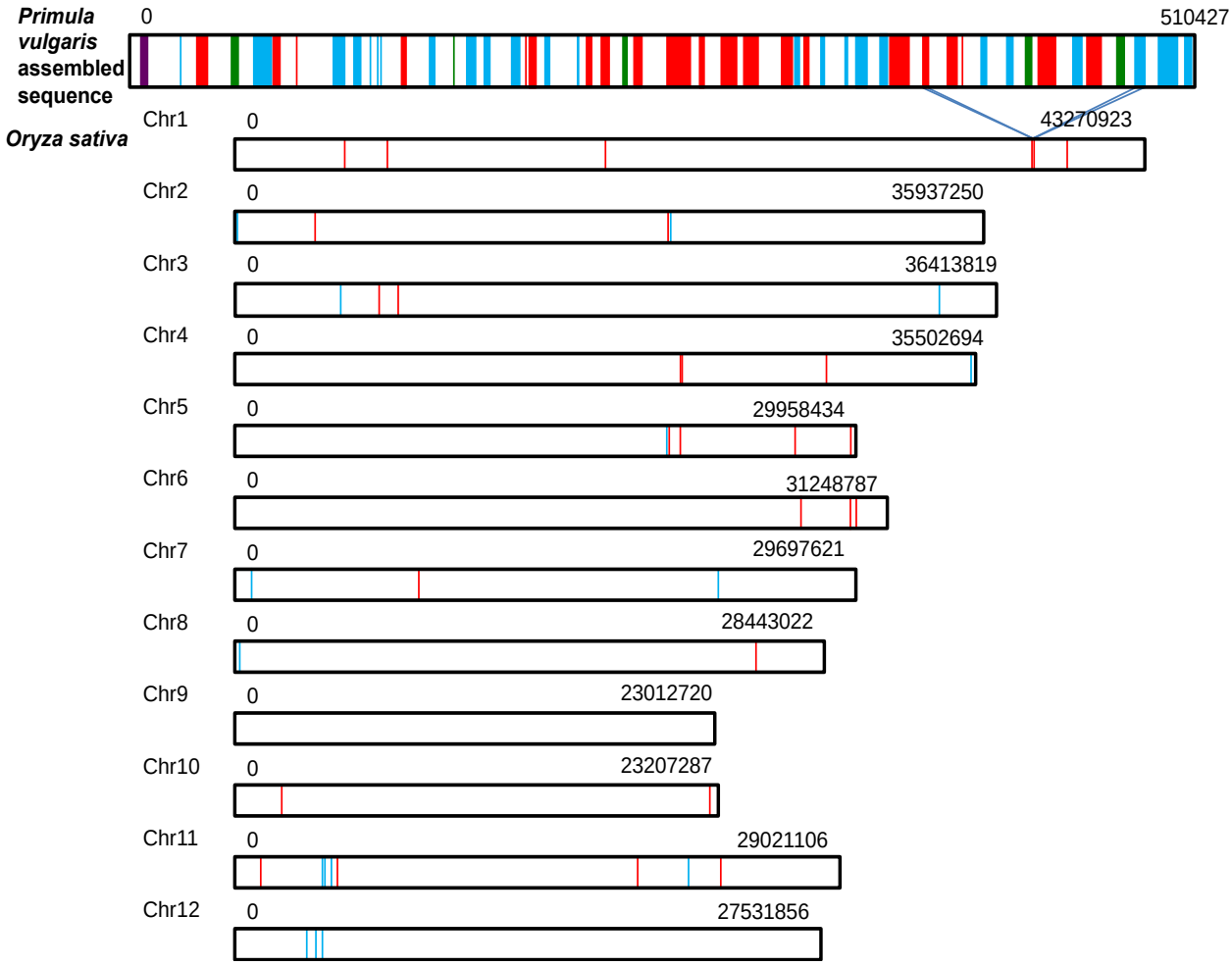
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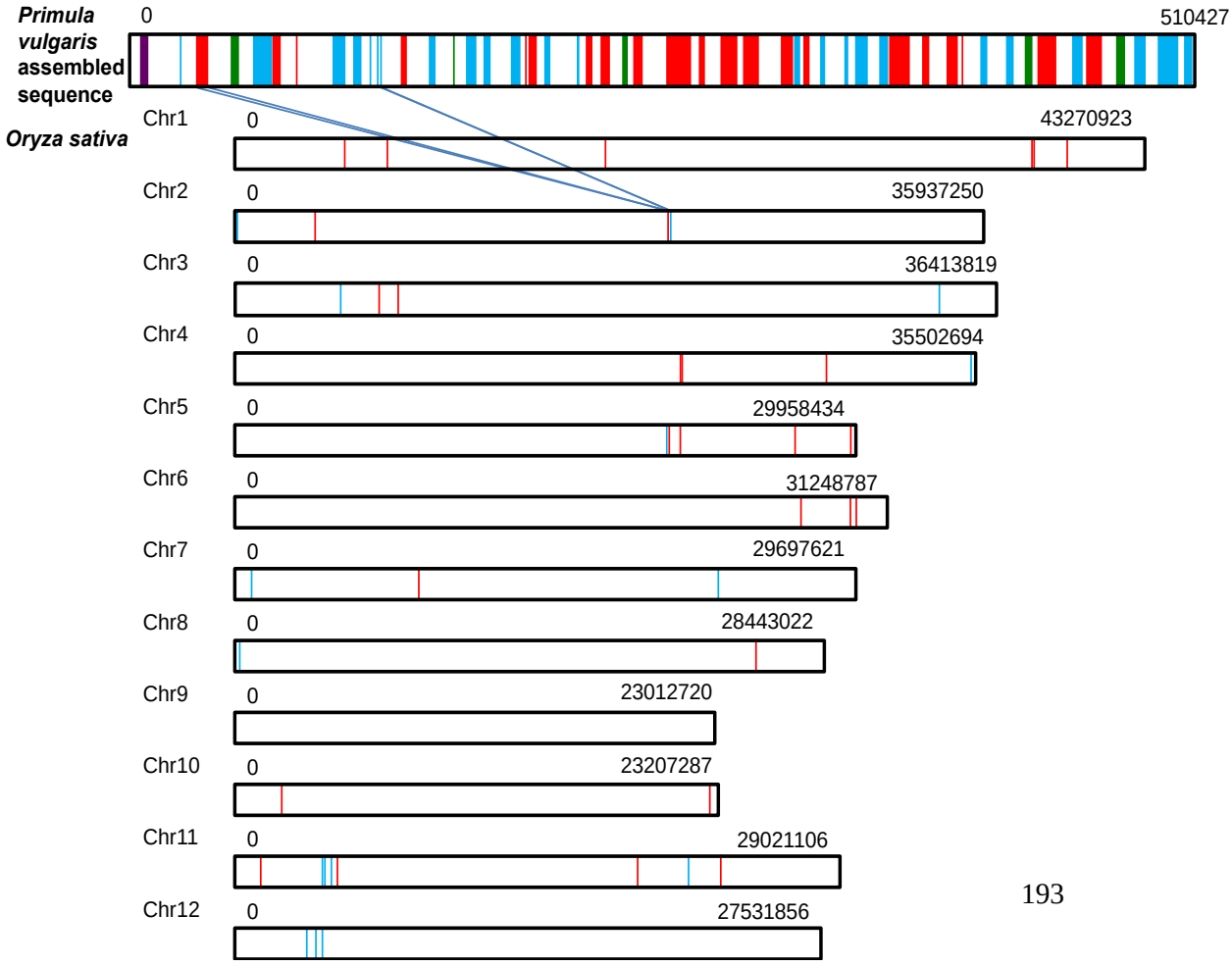
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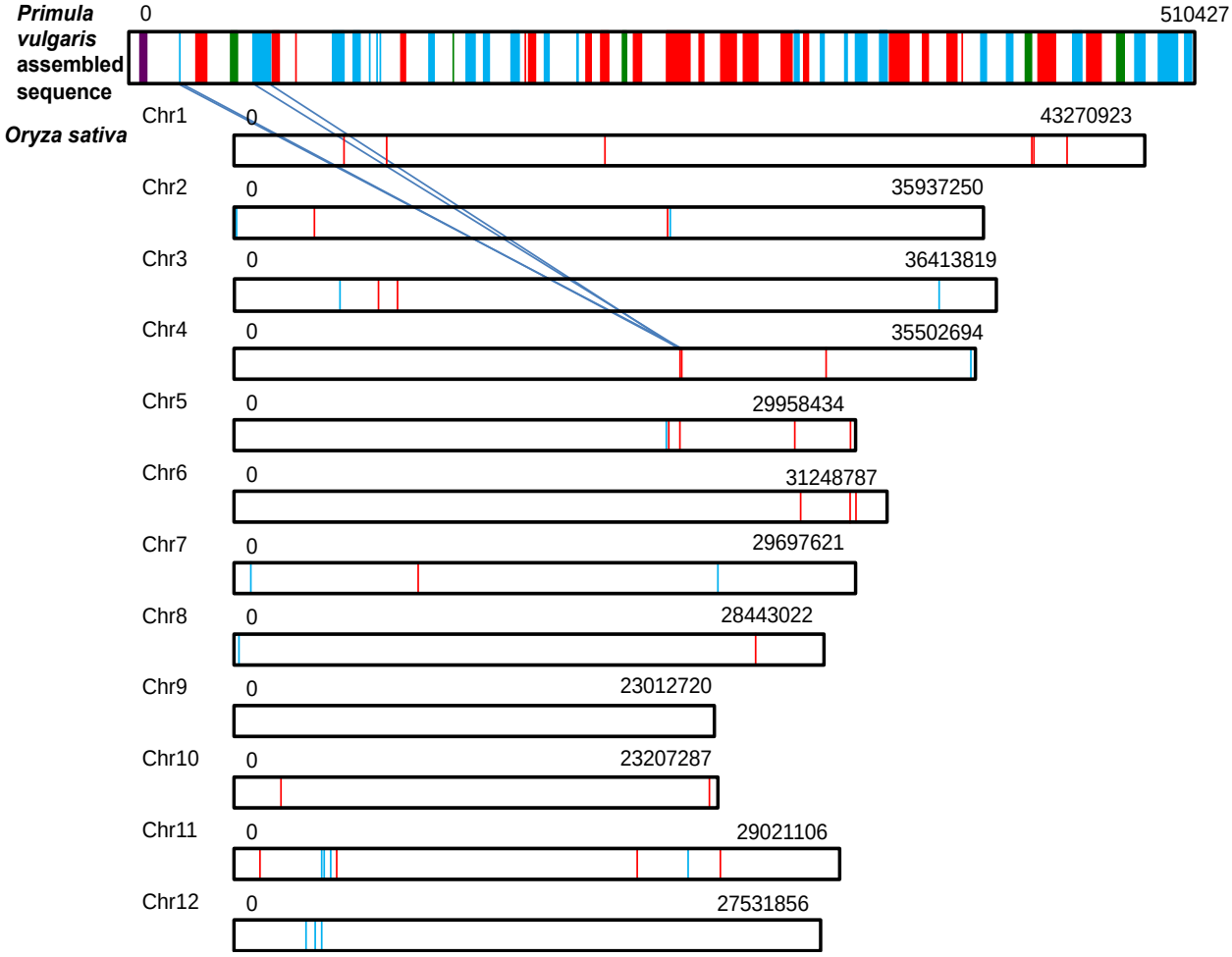
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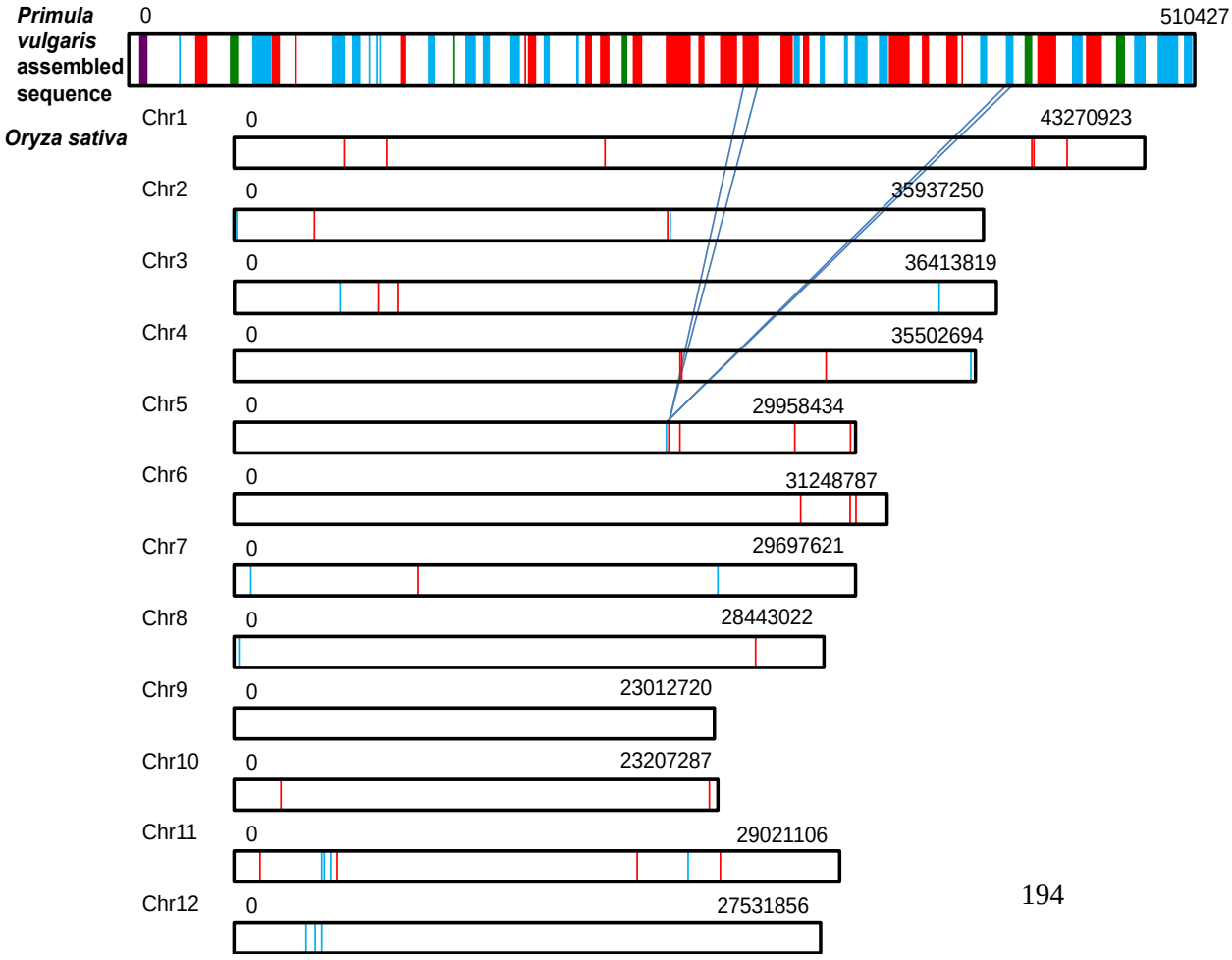
d)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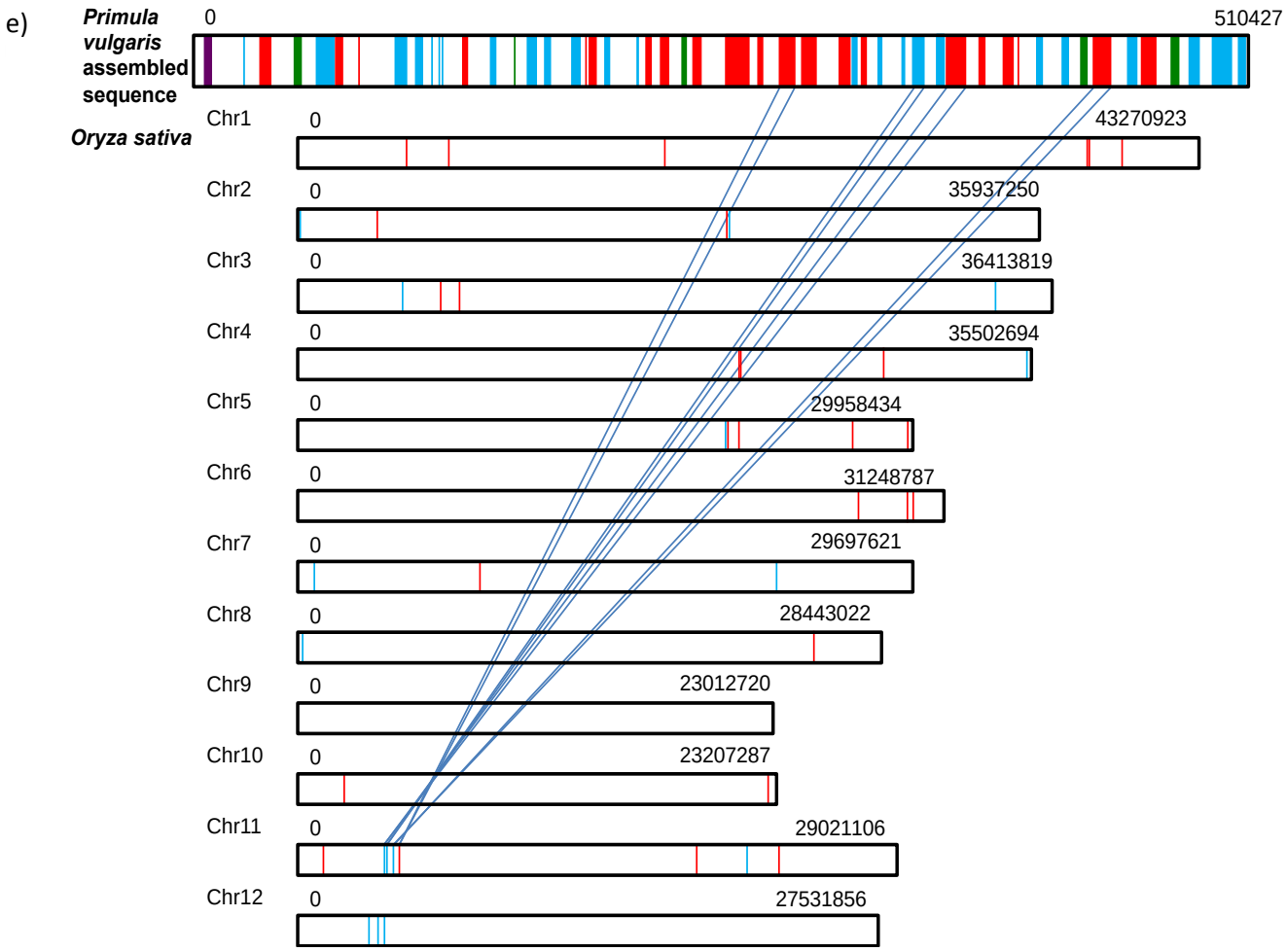

Figure 6.9: Positions of genes found in close proximity in both *P. vulgaris* and *O. sativa*. a) to e) show individual clusters of genes found together in both species.

Figure 6.9a) shows the first such group of genes, identified within Chromosome 1 of *O. sativa* and containing two genes. These two genes, homologues of *PvG39* and *PvG40*, are over 98 kb apart in *Primula* whereas they are within 75 kb of each other in *Oryza*. Additionally, the locus names for these homologues, shown in Table 6.4, suggest that there are a similar number of intervening genes between *PvG39* and *PvG40* in both species. Though Figure 6.9a) shows that the same genes found between *PvG39* and *PvG49* in *Primula* are not found between the two homologues in *Oryza*, this suggests that these two genes have been conserved relative to each other between species. At first, the physical distance between them seems largely

different, almost 20 kb larger in *Primula* than in *Oryza*, but this can be considered a small change relative to the size of the two genomes, with Chromosome 1 of *Oryza sativa* over 43Mb long.

Figure 6.9b) shows another instance of two genes found close to each other in both *Primula* and *Oryza*. *PvG3* and *PvG11* both identified homologues on Chromosome 2 of *O. sativa* and, although these genes are over 80 kb apart in *Primula*, they are within 55 kb of each other in *Oryza*. As discussed above, although this represents a change in physical distance of over 25 kb, this can be considered to be small in relation to the overall size of the *Oryza* genome. Equally, reference to the locus names of both genes in Table 6.4 reveals that there remains a similar number of genes between *PvG3* and *PvG11* in both species. Although it is not clear if the distance between these two genes has increased in the evolution of *Primula* or decreased in that of *Oryza*, this suggests again that these two genes have been conserved relative to each other between the two species.

Figure 6.9c) shows a third pair of genes located near to each other in both species. In contrast to those pairs shown in Figures 6.9a) and b) however, these two genes are found even closer together in both *Primula* and *Oryza.* Although *PvG2* and *PvG5* are separated by 34,152 bp in *Primula*, their *Oryza* homologues are found only 1441 bp apart and, further to this, the locus names shown in Table 6.4 suggest that they are, in fact, immediately next to each other in *O. sativa*. This is particularly remarkable as only two genes lie between the same genes in *Primula*, with one mapping to one of the *Oryza* pseudomolecules as opposed to another chromosome.

The genes highlighted in Figure 6.9d) again show a similar pattern to others discussed already. In this instance, homologues *PvG30* and *PvG43*, two genes over 119 kb apart in *Primula,* have been identified under 36 kb apart within Chromosome

5 of *O. sativa.* Reference to the locus names of the *O. sativa* homologues *PvG30* and *PvG43* in Table 6.4 show that a similar number of genes lie between these two genes in both species, supporting the suggestion that these two genes have been conserved relative to each other but without any conservation of the genes between them.

The final group of genes identified close to each other in both *Oryza* and *Primula* is shown in Figure 6.9e). In contrast to the pairs of genes shown in Figures 6.9a) to d), this group consists of four genes, making it the largest cluster of genes identified within *O. sativa.* However, closer inspection of Figure 6.9e) shows that this cluster in fact contains the pair of genes *PvG36* and *PvG38,* which lie closely together, and the two genes *PvG29* and *PvG45,* which are separated from both these first two genes and each other. Although, alone, *PvG19* and *PvG45* would not have been considered a 'cluster', they have been included as they are still close to each other relative to the large scale of the 29 mb Chromosome 11. Additionally, whilst *PvG29* and *PvG45* appear distant within the assembled *Primula* contig, it must be taken into consideration that the entire 510 kb sequence represents a relatively small region of the entire *P. vulgaris* genome. As such, the identification of these four genes within 145 kb of each other in *Primula* and within 398 kb of each other in *Oryza* can still be seen as significant. Within this group, the pair of *PvG36* and *PvG38* remains the most important, mapping to loci within 11 kb of each other in *Primula* and within 132 kb of each other in *Oryza*. Unlike the examples discussed thus far, in which the number of intervening genes has remained similar in both species, the locus names of the genes, shown in Table 6.4, suggest a much greater number of intermediary genes in *O. sativa*. From the data available, it is unclear whether this is due to a loss of genes by *Primula* or a gain of genes by *Oryza* as the two species evolved separately.

6.3.5 Patterns of genetic distribution identified through syntenic mapping

By using the 51 genes identified and annotated within the assembled *P. vulgaris* sequence as queries with which to search the genomes of different plant species, it has been possible to observe how gene order has been conserved between different plant species. Furthermore, it has also been possible to determine patterns in this conservation and to identify groups of genes that can be found clustered together in other species as well as in *P. vulgaris.*

By selecting the species *A. thaliana, S. lycopersicum, M. truncatula* and *O. sativa* as species for comparison it has been possible to identify trends in the way that gene order has been conserved as the phylogenetic distance from *P. vulgaris* has increased. As the species that is the most closely related to *P. vulgaris*, belonging to the same clade within the Core Eudicots, *S. lycopersicum* showed the highest level of conservation of gene order. Although *PvG1-51* identified homologues throughout the *Solanum* genome, there was a high concentration of homologues on Chromosome 6, with many of the same genes found very close to each other, if not immediately next to each other, in both species. This is significant as it demonstrates that much of the gene order observed in this region of the *P. vulgaris* genome existed before the *Primulaceae* and *Solanaceae* diverged from their common ancestor. As such, the *Primula S* locus must have converged within this region after the *Primulaceae* diverged to become a separate genus.

Although a number of genes were found outside of the cluster seen on Chromosome 5, less than one third of those identified were found away from any other, providing further evidence that the relatively close relationship between the two species had only allowed limited genetic redistribution.

Using Figure 6.1, alone, it is difficult to determine which of the four species investigated shows the second highest level of gene order conservation to *P. vulgaris*. However, through the syntenic mapping of genes *PvG1-51,* it can be seen that a greater conservation of gene order exists between *P. vulgaris* and *A. thaliana* than in *M. truncatula.* As seen in Figure 6.2, when homologues of *Primula* genes were identified and mapped in *Arabidopsis,* a number of them were found on Chromosome 1. Although some homologues were found on each of the other *Arabidopsis* chromosomes, there is a clear concentration of them in this single area. Further to this, many of the genes identified within these clusters, were found in similar clusters within the *Primula* sequence. Through comparison of Figure 6.2a) and Figure 6.3a), it is clear that the same level of conservation has not occurred in *Arabidopsis* as was seen in *Solanum*. Similarly, further comparison with Figure 6.4a) shows even less conservation of gene order between *Primula* and *Medicago,* and no clear concentration of genes is seen within a single chromosome. As such, this suggests the *A. thaliana* is more closely related to the *Primulaceae* than *M. truncatula.*

The three species discussed so far show differing levels of synteny when compared to the assembled *P. vulgaris* sequence, typically demonstrating a larger change in gene order as the two species have become increasingly distant. However, *S. lycopersicum*, *A. thaliana* and *M. truncatula* remain relatively closely related to *P. vulgaris* within the plant kingdom. Mapping homologues identified in *O. sativa,* a monocot species, has allowed for comparison with a much more distantly related species. Although a number of clusters of genes were identified and presented in 6.3.4, the majority of these comprised of only two genes while the final cluster, though consisting of four genes, contained two that were far enough removed to be

considered isolated. Although each gene within these pairs appeared to maintain a similar relationship to its partner in both *Primula* and *Oryza*, the spread of other genes throughout the genome suggested that little conservation had occurred. As a result, and in contrast to the eudicot species discussed, any preservation of gene order between *Oryza* and *Primula* appears to be due to mechanisms specific to pairs of genes, as opposed to a wider conservation that also included their surroundings.

The results discussed in this chapter shed light on the distribution of 51 genes adjacent to the *P. vulgaris S* locus. In particular, they demonstrate that the genes in this region can also be found in a similar order in other species. As the phylogenetic distance between *P. vulgaris* and other species grows, the level of conservation seen diminishes. Significantly, a particularly high level of conservation exists in the order of these genes between *Primula* and *Solanum*. This synteny between the two species shows that the gene order described in Chapter 5 must have existed prior to the divergence of the *Primulaceae* and the *Solanaceae* from a common ancestor. Consequently, this gene order must also have existed before *G*, *P* and *A*, the key genes of the *S* locus, settled in this region; a discovery that will play a significant role in the work to determine the evolutionary origin of the *S* locus.

CHAPTER SEVEN

General Discussion and Conclusions

7.1 General Discussion and Conclusions

There are a number of other species, both plant and animal, which demonstrate tight linkage between multiple loci. 'Supergenes' such as these are commonly found on sex chromosomes but a number of autosomal supergenes have also been documented, each demonstrating restricted levels of recombination (Lewis, 1942; Charlesworth, 1996; Schwander *et al*., 2014). Examples of these include supergenes regulating Batesian mimicry in butterflies, plumage polymorphisms in *Zonotrichia albicollis* (white-throated sparrow) and shell colour in snails, as well as heteromorphic self-incompatibility systems like that seen in *Primula* species (Murray and Clarke, 1976; Joron *et al*., 2006; Thomas *et al*., 2008; Schwander *et al*., 2014).

Furthermore, it has also been demonstrated that certain areas, such as those near to centromeres, also show low levels of recombination and closer inspection of many supergene loci has shown that they are often located in this region (Nachman, 2002; Schwander *et al*., 2014). As the distance from these regions increases, the genome becomes more exposed to recombination. As a result, the areas immediately surrounding these protected regions are of great interest, in particular when examining the genes that are located there. Whilst McCubbin and Kao (1999) have stated that, in order for an *S* locus in any species to be functional, recombination must be suppressed, this is seen to differing degrees. In *Brassicaceae*, it has been shown that although the region immediately surrounding the *S* locus may be highly

polymorphic, the region between SLG and SRK (the female determinant) is strictly protected from recombination (Casselman *et al*., 2000; Shiba *et al*., 2003). Similarly, it has long been demonstrated that a very low rate of recombination exists within the *S* locus of *Solanaceae* species (Clark and Kao, 1991).

Heteromorphic species such as *Primula vulgaris* often demonstrate a tight link between heteromorphy and self-incompatibility, adding an extra layer of complexity to that which is seen in monomorphic self-incompatible species. As such, this conserved region of the genome, strictly protected against recombination is all the more interesting and, subsequently, so is the region surrounding it. The work described in this thesis has provided an important insight into this region immediately adjacent to the *P. vulgaris S* locus, successfully meeting the majority of aims set out in 1.8.

The initial aim of this project was to assemble a single contiguous sequence that could connect a number of genetic markers located on the *A* side of the *S* locus. The initial approach taken to this was to use sequence data from the *P. vulgaris* var. Blue Jeans BAC library to construct a sequence that joined the two markers *PvSLP1* and *PvGLO*. However, in order to generate a sequence that could be used reliably, it was important to use BACs that had all been derived from the same allele of the *S* locus. Chapter 3 describes the steps taken in the attempt to determine which BAC had been derived from each allele.

As discussed in 3.3, analysis of key BACs that would serve to provide a link between the two genetic markers generated mixed results. Although some BACs, such as 81B15, could be confidently attributed to the Thrum allele through the presence of the Thrum specific marker *PvSLP1* as well as Thrum specific restriction sites, others could not be so easily assigned. For example the opposing ends of the

BAC 28O8 demonstrated homology to different alleles, suggesting that a recombination event had occurred within the region covered by the BAC. Further to this, data attained through the direct sequencing of PCR products conflicted with data attained through whole genome sequencing. As such, it was concluded that, although the BAC sequences could be used as a scaffold for the assembly of further sequence data, the BAC data itself would be unsuitable as a tool for the annotation of this regions, as any genes identified could not be attributed to either Pin or Thrum allele.

As described in 4.2.1, the BAC sequence data was subsequently used in this way, generating a single contiguous sequence that connected the two genetic markers PvSLP1 and *PvGLO* in the *P. vulgaris* cv. Blue Jeans genome. Subsequently the availability of wild type genomic sequence data, sequenced and assembled concurrently with the work described above provided the further data necessary to expand on this. Genomic sequence contigs, sequenced from wild type Pin individuals, could then be assembled together using the already assembled BAC sequences as a scaffold (see 4.2.2). While this change in DNA source, from a cultivated variety to wild type, inevitably led to differences between the scaffold and the sequences assembled against it, it was an essential step to ensure that the subsequently assembled sequence was as a true a representation as possible of the *P. vulgaris* genome. Furthermore, as discussed in Chapter 4, the use of genomic sequence data allowed for a great expansion of the sequence already assembled. The increased coverage afforded by whole genome sequencing, as opposed to the contigs assembled through the sequencing of discreet BACs allowed the construction of a sequence that not only joined the two markers PvSLP1 and *PvGlo*, but also extended to include *PvSLL1*. As a result the assembled sequence that physically connected a

gene that was tightly linked to the Thrum allele of the *S* locus (*PvSLL1*) and one that was known to recombine with the locus (*PvGLO*).

While this new sequence data provided a new insight into this region immediately adjacent to the *S* locus as per the first aim of this project outlined in 1.8, unfortunately it was not complete, with the sequence data instead assembled into three contigs that collectively spanned the region (named Seq1, Seq2 and Seq3). Although gaps remained between these three contigs, alignment of known BAC end sequence to Seq1, Seq2 and Seq3 revealed that the gaps between them were very small, according to the predicted lengths of the BAC ends used. As such, although it is thought that very little genomic data has remained unassembled within these gaps, it is hoped that the continued generation and assembly of genomic sequence data will help to bridge these and join the three sequences together.

Once assembled, Seq1, Seq2 and Seq3 provided a unique opportunity to identify the genes that were located within this region of the *P. vulgaris* genome and the chance to meet the second aim of this project, as described in 1.8. A total of 51 genes, serving a variety of functions, were identified within this region. While some of these were previously known, such as *PvG2* (*PvSLL1*) and *PvG49* (*PvGLO*), the majority of these were identified within *P. vulgaris* for the first time. As stated in 1.8, it was hoped that the annotation of the genes in this region would aid in the identification of *sepaloid*, especially as linkage data (such as that shown in Figure 1.5) suggested that it might be located in this area. However,, no reliable candidates were identified and the possibility that *sepaloid* is located in a different region of the genome must be considered.

The final aim of this project was to use the annotations discussed above in order to examine synteny between this region of the *P. vulgaris* genome and those of other

plant species. Through the identification of homologues of *PvG1-51* on the comparison species *A. thaliana*, *S. lycopersicum*, *M. truncatula* and *O. sativa*, each of the genes annotated in Chapter 5 were successfully mapped across these four species. The levels of synteny observed between these species and *P. vulgaris* was intriguing, particularly in *S. lycopersicum*, in which a very high level of gene order preservation was seen. This was of particular interest as it suggests that this gene order seen in *P. vulgaris* must have existed prior to the divergence of these two species and, subsequently the formation of the *S* locus. This conclusion is of great import as it provides an insight into the age and evolution of the locus as work continues to identify the genes the comprise it.

Appendix A

Details of all primers used, including primer sequence and the melting temperature (Tm) as determined by the manufacturer. All primers were synthesised by Eurofins MWG Operon.

Chapter 2

The following primers were used to amplify and sequence inserts from plasmids generated using the Promega pGEM-T Easy Vector System.

Primer Name	Primer Sequence	Tm (°C)
SP6	TATTTAGGTGACACTATAG	42
T7	TAATACGACTCACTATAGGG	43

Chapter 3

The following primers were used to amplify the BAC end sequences from each BAC.

Primer Name	BAC	End	Primer Sequence	Tm (°C)
6K4.RF	6K4	R	AAATCACACAGTGGCCCTTTA	59.5
6K4.RR	6K4	R	CCTATTTGCGCATTTTTGGT	60.0
60I18.FF	60I18	F	GGAAACGAAGGTTTGCTCTG	59.9
60I18.FR	69I18	F	CAACCCAAAAGGTGTAGTTGG	59.4
71C24.FF	71C24	F	GTGAAGGGTTTGCACTTGCT	60.3
71C24.FR	71C24	F	CCTTTCGAAAAGTGGTCCAA	60.1
28D21.FF	28D21	F	GCGGCGGGTAACTTTGATA	61.0
28D21.FR	28D21	F	TGAGCTTATGAGTTTGCGAAAG	59.7
20E12.FF	20E12	F	TTTTGGGCATTGTTTTTCAA	59.0
20E12.FR	20E12	F	AAGGGGATGCATAGTTGCAC	60.0
65K20.RF	65K20	R	AAAGGCACTGATACGGGATG	60.0
65K20.RR	65K20	R	ATGAAGGTTGATTGCGTTCC	59.9
51M17.FF	51M17	F	ATTGCGTTCCGTATTGGTTC	59.8
51M17.FR	51M17	F	ATTTGTTTGGTGGTGGTGGT	60.0
81B15.FF	81B15	F	GCGGGAAGTAGTGGAACAAA	60.1
81B15.FR	81B15	F	CAATCTGAGCCGTGGTTACA	59.7
81B15.RF	81B15	R	GGTGCAAAAGCAAAAGCACT	60.4
81B15.RR	81B15	R	ACAAACTTGGTTGGGCAAAT	59.3
46P3.FF	46P3	F	TCGGGAGGCTGAAAATTGTA	60.6
46P3.FR	46P3	F	CCATAAACTACGTGATTTACTTTTGAA	59.1
46P3.RF	46P3	R	TTTATAACTAACGGGGCCACA	59.4
46P3.RR	46P3	R	TCTGATTCCGTCACTGGATG	59.6
9B24.FF	9B24	F	ACCCAATGTGCTGGAAAGTC	60.0

9B24.FR	**9B24**	**F**	**AACAAAGCCAACGGTTCAAG**	**60.1**
9B24.RF	**9B24**	**R**	**ATGACGAGGCGGATACTGAC**	**60.1**
9B24.RR	**9B24**	**R**	**ACGACTGGTGTGAACGGAAT**	**60.4**
28O8.FF	**28O8**	**F**	**AGGGAGGAGGCTTTGACACT**	**60.3**
28O8.FR	**28O8**	**F**	**AAAAGAAAAACCCACGCAAA**	**59.6**
28O8.RF	**28O8**	**R**	**CGACCAAATATGGTGGCTCT**	**60.0**
28O8.RR	**28O8**	**R**	**GGGATGAGTCTCCAAAGCAG**	**59.8**

Chapter 4

The following primers were used to orientate contigs within the BACs 81B15, 46P3, 9B24 and 28O8.

Primer Name	**BAC**	**Sub-contig**	**Primer Sequence**	**Tm (°C)**
2A4R1	**81B15**	**4**	**CCGGATTTTAGGGTTTTGCT**	**55.3**
2A7F1	**81B15**	**7**	**GGAGCTACAGGTCCGAACAC**	**61.4**
2A9R1	**81B15**	**9**	**TGCATGTGGGTGAATATTTAGA**	**54.7**
2A9F1	**81B15**	**9**	**GCGAAACGAGACTGTCATTG**	**57.3**
2B1R1	**46P3**	**1**	**ATTTTCAGCCTCCCGATCA**	**54.5**
2B2R1	**46P3**	**2**	**TCGAGCCATATTATTTTCCTGT**	**54.7**
2B4R1	**46P3**	**4**	**AGAATGCTGAAGTGGGCTGT**	**57.3**
2B4F1	**46P3**	**4**	**CAGATTTGTTCTTGCTTTTTGG**	**54.7**
2B6F1	**46P3**	**6**	**TCAAGCCAACGATGCATAAC**	**55.3**
2B6R1	**46P3**	**6**	**TGTGACTGGTGCTTGTTTGG**	**57.3**
2B7F1	**46P3**	**7**	**TGTGACTGAAATCAGTAGAGAGAGAGA**	**61.9**
2B7R1	**46P3**	**7**	**AATAAAAATGTCAAAATCCAAAAGA**	**51.5**
2B11F1	**46P3**	**11**	**CCAATTTCAATTCCAATGCAC**	**54.0**
2B11R1	**46P3**	**11**	**TCTGGAAAATAATCGACACTGC**	**56.5**
2C10R1	**9B24**	**10**	**CACAGCAAGTTGGGATCGTA**	**59.7**
2C11F1	**9B24**	**11**	**TTTTGCGTTTTCGGATTTTT**	**49.1**
4A1F1	**28O8**	**1**	**GCACCTTGTCCCTTCTACCA**	**59.3**
4A1R1	**28O8**	**1**	**TCACATATCACCAACGACTGC**	**57.9**
4A2F1	**28O8**	**2**	**GCTTGTGGGGATTTAATGTGA**	**55.9**
4A3F1	**28O8**	**3**	**CCCTCATGGAGACTGCACTT**	**59.4**
4A3R1	**28O8**	**3**	**CAATGTACTTGGGCACCTGA**	**57.3**
4A4R1	**28O8**	**4**	**AGCGTTCTTATGGAGCAGTTG**	**57.9**
4A7F1	**28O8**	**7**	**ACCCGCAGCGAATGATAGTA**	**57.3**
4A7R1	**28O8**	**7**	**CCGGTTTTGTAGACCAACCA**	**57.3**
4A9F1	**28O8**	**9**	**TTGAACCTTAACTCTTTTCTGCCTA**	**58.1**
4A9R1	**28O8**	**9**	**CTGGCTTCTTGCGAAAACAT**	**55.3**
4A11F1	**28O8**	**11**	**TTTTTGCCAGTTTTGTGACC**	**53.2**
4A11R1	**28O8**	**11**	**TTTGTTGAAATCGCCGTATG**	**53.2**

Chapter 5

The following primers were used to amplify the 3' regions of genes *PvG1-PvG51*

Primer Name	Gene	F/R	Sequence	Tm (°C)
PGP1.F	*PvG1*	F	CAAACATACAGCACGGGAAA	59.6
PGP1.R	*PvG1*	R	GAGCGTCATATGCAGTGGAA	59.8
PGP2.F	*PvG2*	F	CGTGGTCATATTCCAGCAAA	59.5
PGP2.R	*PvG2*	R	TCTGCACACAAACACAAAAGAA	59.4
PGP3.F	*PvG3*	F	AAGACGTAACTCGGCAAAGC	59.5
PGP3.R	*PvG3*	R	TTTGGGAATGATATCCCTTGA	59.2
PGP4.F	*PvG4*	F	TGATTTGAACTCTGGCGATG	59.8
PGP4.R	*PvG4*	R	TGGTGTTCTGCATTTGCTTC	59.8
PGP5.F	*PvG5*	F	CTCAAATCACGCGATTCCTC	60.7
PGP5.R	*PvG5*	R	CTCGTGAACGCTAATTGCTC	58.7
PGP6.F	*PvG6*	F	CCGGCACTCTTTAACTGGAA	60.2
PGP6.R	*PvG6*	R	AGTGAGTCGGCATCGACTTT	59.9
PGP7.F	*PvG7*	F	CTTGCTTGCACATTCGAGTC	59.6
PGP7.R	*PvG7*	R	ACCTGATCCCGGTTTCTCTT	59.9
PGP7.F	*PvG8*	F	AAAAGGTCCCAAACCACCTC	60.2
PGP8.R	*PvG8*	R	CACAACAAAAAGGCAAGAAGG	59.8
PGP9.F	*PvG9*	F	TATTGCTAAGGGGACGTTGC	60.1
PGP9.R	*PvG9*	R	GGGTTCTAGCCAAAACAAGC	58.8
PGP10.F	*PvG10*	F	TATTGCTAAGGCGAGGTTGC	60.4
PGP10.R	*PvG10*	R	AAAACGCAACGAAAAACCAC	60
PGP11.F	*PvG11*	F	CCAAGGTCGCGAAAACATAG	60.6
PGP11.R	*PvG11*	R	AAGCAAGCATGATGCGATAA	59.4
PGP12.F	*PvG12*	F	CAGTACTGCAGGTCGTGGTG	60.4
PGP12.R	*PvG12*	R	TGGCTCATCTCTGGGAGGTA	60.8
PGP13.F	*PvG13*	F	TCGGTTTTTCGGTTTCAGTC	60.1
PGP13.R	*PvG13*	R	CCTGCAACTGTACCTGCGTA	59.9
PGP14.F	*PvG14*	F	GGGTGTTTTGTTTGGGATTG	60.1
PGP14.R	*PvG14*	R	TCCAATGACTGCAAATGGAA	60.0
PGP15.F	*PvG15*	F	AATTGAAGATGGCGGAAATG	59.9
PGP15.R	*PvG15*	R	GGGTTGTAACGGGTTGTGAC	60.1
PGP16.F	*PvG16*	F	TCGGATGAACTTGCTCTCCT	60
PGP16.R	*PvG16*	R	AGCCTTGGCCCAGTAAAAAT	60
PGP17.F	*PvG17*	F	GTTGCCAATGGGTGGATAAG	60.2
PGP17.R	*PvG17*	R	AATTTGCAAGTAATCGGTCACA	59.5
PGP18.F	*PvG18*	F	GATGATAAATGGGGCAAACG	60.2
PGP18.R	*PvG18*	R	TCACAGGGCAAAATCACAAA	60.1
PGP19.F	*PvG19*	F	TTTGTGATTTTGCCCTGTGA	60.1
PGP19.R	*PvG19*	R	TTCGGGGTTCAAGTTTTGTC	59.9
PGP20.F	*PvG20*	F	GTTGACTTTTGGCCATCACC	60.4
PGP20.R	*PvG20*	R	GCTGCCAGGTGCTTATATGG	60.6
PGP21.F	*PvG21*	F	ATTGACCATGCCCAAGAATC	59.8
PGP20.R	*PvG21*	R	TCAAATCGGAGCACTCAAAA	59.4
PGP21.F	*PvG22*	F	GGATGTGATCGCCAAGTACA	59.5
PGP22.R	*PvG22*	R	CGCACCCTAAAGAATAGTGGA	59.2
PGP23.F	*PvG23*	F	CCAAAACTGAAAAGCTAACCAAA	59.7

PGP23.R	***PvG23***	**R**	**GCCATCAAATGGAAATGGAA**	**60.6**
PGP24.F	***PvG24***	**F**	**ACCCCAAGAAAAACAAGCATT**	**59.9**
PGP24.R	***PvG24***	**R**	**TTCGGTTTGTGATCGTCAAG**	**59.7**
PGP25.F	***PvG25***	**F**	**AGTGCGCTAAGAACCTCACC**	**59.5**
PGP25.R	***PvG25***	**R**	**CAAGCTATGATTCTCTCGCAAC**	**59.1**
PGP26.F	***PvG26***	**F**	**ACCACCGGTTCTGACTATGC**	**60.0**
PGP26.R	***PvG26***	**R**	**CTAAGTTGGGTCGTGTTGGG**	**60.4**
PGP27.F	***PvG27***	**F**	**GCTCACAACAAACCCTGACA**	**59.7**
PGP27.R	***PvG27***	**R**	**AGTTTGGGATGCCGAAAATA**	**59.4**
PGP28.F	***PvG28***	**F**	**TTAGGAGGGACCATCAATGC**	**59.9**
PGP28.R	***PvG28***	**R**	**TGAGTGGTTGAGTGATAATCTGTT**	**57.8**
PGP29.F	***PvG29***	**F**	**AAACCACAGGCTGATTTCCA**	**60.5**
PGP29.R	***PvG29***	**R**	**CGATGGAGATCGTACCAAAGA**	**60.1**
PGP30.F	***PvG30***	**F**	**TGCAAATGTCATTGCTGGAT**	**60.1**
PGP30.R	***PvG30***	**R**	**CGGGTTTGATCCCAATTTTT**	**60.9**
PGP31.F	***PvG31***	**F**	**CTCGGGAGCATATTCCCTTT**	**60.4**
PGP31.R	***PvG31***	**R**	**AAAATCGCGCAGAAAAACAT**	**59.7**
PGP32.F	***PvG32***	**F**	**AAAACGAGCCTCCGGAAC**	**60.2**
PGP32.R	***PvG32***	**R**	**TGGGTGTTGTTTTGTGAGGA**	**60**
PGP33.F	***PvG33***	**F**	**TGTGCAGTGTTGGAGAGTCC**	**59.9**
PGP33.R	***PvG33***	**R**	**CTTCCTGAAAGAGCACCTCAA**	**59.6**
PGP34.F	***PvG34***	**F**	**GTGTGCCCAAAATTGGCTAT**	**59.8**
PGP34.R	***PvG34***	**R**	**CACTACTTCCCGCTTCCATT**	**59.2**
PGP35.F	***PvG35***	**F**	**CAGTTTCGAACCGGTATAAGC**	**58.8**
PGP35.R	***PvG35***	**R**	**TGATGGACAATGTCGGAGAA**	**60**
PGP36.F	***PvG36***	**F**	**CCTCCCTACACACCCAAGAA**	**60**
PGP36.R	***PvG36***	**R**	**TCCTTTCCTCCTCTTGTTTAGC**	**59**
PGP37.F	***PvG37***	**F**	**ATTGCGGCAGGCTTTGTAG**	**61.3**
PGP37.R	***PvG37***	**R**	**CCCTCTTCTTGAATGCACAA**	**58.8**
PGP38.F	***PvG38***	**F**	**CCCTCATCTCTATAGCAACTCTTG**	**58.6**
PGP38.R	***PvG38***	**R**	**TGCAACTCTTTCTCAAAAGCAA**	**60.2**
PGP39.F	***PvG39***	**F**	**GCAGTAGCCAAATTGCAACA**	**59.9**
PGP39.R	***PvG39***	**R**	**ATTTCGTCTCACCGTTCCAG**	**60.1**
PGP40.F	***PvG40***	**F**	**CGGACTTGTCATGAGCTGAA**	**60**
PGP40.R	***PvG40***	**R**	**GTCGTATCGGCATGGAAACT**	**60**
PGP41.F	***PvG41***	**F**	**GGGAGCCACCAAAAACACTA**	**60**
PGP41.R	***PvG41***	**R**	**CCAAGAAAAGCGGCAAAATA**	**60.2**
PGP42.F	***PvG42***	**F**	**TCCTCCCTCTATACCGTTGG**	**59.0**
PGP42.R	***PvG42***	**R**	**GGGATTGAGCATCCAAAATG**	**60.3**
PGP43.F	***PvG43***	**F**	**AATCGTATGCGCCATTCAAG**	**61**
PGP43.R	***PvG43***	**R**	**ATGGTAGCATGAGCGGGTAA**	**60.5**
PGP44.F	***PvG44***	**F**	**CGATAGGCAATTAGCCGATATT**	**22**
PGP44.R	***PvG44***	**R**	**TTTGATAGCCTCAGAATTTTTGAAT**	**25**
PGP45.F	***PvG45***	**F**	**AAGTTGGCTTGAACGGGATT**	**60.9**
PGP45.R	***PvG45***	**R**	**GGTTCCACAGCTTGATTCGT**	**60.1**
PGP46.F	***PvG46***	**F**	**AACCTCCAAGACCCCAGTTC**	**603**
PGP46.R	***PvG46***	**R**	**ACAATGTCCAGCAAGCTTCA**	**59.4**
PGP47.F	***PvG47***	**F**	**CCCCTCACTTGTAACCCAAC**	**59.3**
PGP47.R	***PvG47***	**R**	**AAAAACGCTGAAATGGCTTC**	**59.3**
PGP48.F	***PvG48***	**F**	**AAGACAAGTGTTTTATCTGGATCAT**	**57.4**
PGP48.R	***PvG48***	**R**	**TGGTATAGCTCGACACAGCA**	**58**
PGP49.F	***PvG49***	**F**	**GGATATAGAAGGCGGGGAAA**	**60.2**

PGP49.R	***PvG49***	**R**	**AGGCATTGCGTAATCCGTA**	**59.2**
PGP50.F	***PvG50***	**F**	**GGATTAGGGGTTTTCGGGTA**	**60**
PGP50.R	***PvG50***	**R**	**CGGGAGTACTTGCAACAAAAA**	**60.2**
PGP51.F	***PvG51***	**F**	**ACGCGAACAAGAGGAGTCAT**	**59.9**
PGP51.R	***PvG51***	**R**	**TGTATCGGTGTTTCCTGTGC**	**59.6**

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Appendix B

Sequence of the assembled *Primula vulgaris* contig. Sequence was constructed using genomic data from a Pin individual between the markers *SLL1* and *PvGLO*

Sequence Length: 510,427 bp.

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GGAGATTTGCATTAATCAAATCTTGATTTGGAGCGTTTTTGCAAAAAAGTGTCCAAGTTGATGTCTAA
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TTTTGTCAGGGTGACTTCCATGCTGGGATGAACTTTGCAGCAGTAATGGATGCGCCTGTTATTTTCTT
CTGCCGAAACAATGGGTGGGCCATAAGCACTCCTATTTCCCAGCAGTTTCGAAGTATTTCTCGTTGTC
AATAACAATTGTATTGATTTAAAGTTAATATGATCATTTTGCTTCACTTTTCATTTATTTGGTCATTG
CTTACAAGTTTATTCCCATTTCTATTGCCATTTCTCTTAATCTATCATCCGCGGAAACAAAAGGAGTA
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TTTTTTTGTTCTTACAACAGGTGATGGAGTTGTTGCTAAAGGTCAAGCCTATGGAATCCAAAGTATTC
GGATAGATGGGAACGATGCACTTGCTGTTTATAATGCCATAAGAGCAGCACGTGAAATAGCAATCACT
GAACAAAAGCCCATACTGATTGAGGTGCATCTTGTTTCTTGTTTCAAAAATCTGATTTTTCTCCCTTT
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CAAGAGAAGAAAAATCGACACACACATCTTAATTACTGAACCATAACAACTGAAATTTAAATTATCTA
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CAGTTGCAAGATTTAGAAAATGGGTCGATAGAAATGGTTGGTGGACCGATAAAGACGAATCTGATCTT
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AACACATCAGTAATCCAGAAATTCATTCGTCACAAAGCGTGTCCATATGATGTTTAGTTCGAAGCATA
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GTGGGGCTGGAGTTCCCTGAGAGACGAGGCAAAGGAGTATAATCAACTTACCAACTGTCGTGGTTAGT
TTACAAGTACTCAGGCCTTGTTCGGTTGTGGCCGGTAGTAAGAGTTCACGAGGGGTTATGCTTAGACA
ACAAAATACCATTTCAATCCCATTTCCATCGACTGGTCCCAACTCCTTAACTGGCGAGGGGATGTCGG
CACCCCCTCGTCCGGACCGATATCAACTCCACAGCAGGCGATCCGGGCCTGTCAACCATGGGTAACGC
GTCACCCCGGATCTTGAAGGGCCGGACCGTGTCTAGGCCGGCCCGGAGAAGCTTGTCGAGCACACTTC
CCCAATTAATGTTGCTGCT

Appendix C

Genomic DNA sequences of 51 genes identified within the assembled *Primula vulgaris* sequence. All sequences include 500bp at both 5' and 3' ends of gene. Exons are shown in red. Orientation of genes within the assembled sequence is also shown.

PvG1 (+/+)

ATTACACATCGATACATGCACTCATACGTAAAAACCCTAAAAGATCCACACTTCTTACAACTCCTCTC
GACGAAAAAGTATGAACGGTAGTAACTCTGCCAAGATACACTTGATCTTTGCTATTAATTGTCCAGGC
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AGTTTGGTGTGGAAAATATAGTAAAACTTTTATAAATTAATAATGTTGGTAGCATGAATATTTATTAA
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AATATACTTGTTCATAACATAAATTAACTTATTATAATTATTAATAATATTCGCTAAAATTATTAGTA
AAGTCAAATACACTAATTCATCTAACCGTATATAAATTTTGTTACATATTAAACCGTTTAGCAAACTA
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TTGTGACATTTTTTAACTCTCATTAAATCAAACATTATTTTGTAGTGCTCGTTAACTATAAATGCTTC
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TCAATGTAACTGTTCCGTCAAATCGCAAGCTGAACTTATCACTATAAAATAATTTTTGATTTAATAAG
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ACTGTCACAAAACCGTCACAAAAACCGTCGCTAATAAACTCGTAACAAAAAATATCATCACTAATCCC
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CTTCTGGACACGACTCGTTTTCAACATTTACTTGGCCAAATTCTGTCGACGTTTTTGACCAATACTAG
CCAAAATCCAACTACGAATTAAGGTTCTAACAGTAATCAATTTAACGATCTCATTATCCTTAAGGGCA
ACCCAACCGGTTATAGCATGTCCTACTATATATATTGTATCTTGAACTTTGCTTAATTACCGGTTTCA
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CAATTAATTGTCCATTACGAAACTACGTACAATTTTAACCGGCCAATAGCTTATGTCAAAATTGTCGG
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GCATAGTATATTCCACATGTACACATGTACTTATCTGACATTTTCCCAAACTCTTACCTCCTAATATT
CCACTGCATATGACGCTCTTTTTTTACAAGAAAAAATTATACAGTATATTTTTGGTCCAAGTAAA

PvG2 (+/+)

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GAGATTTTTTTTGCTATGATTGCTTAAAATTTAAAATCCAATAAGTCACCTTTCAAGAGTGAATATTT
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PvG3 (+/-)

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AAAGTTTTGAGCTAATGTTAGAAAACCAGTGTTATGGACACAAAAACTCGCACGAACATCAAGACAGC
ATACGA

PvG4 (+/-)

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PvG5 (+/+)

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PvG6 (+/-)

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PvG7 (+/-)

TAGCATTCCTCTAAAAAATAATGACCCCTTCTTGTTTTGTAAATTTGGTTGGATAGATTTAAAAAGAA
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PvG8 (+/+)

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PvG9 (+/+)

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TAGTT

PvG10 (+/+)

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TATTTTATAAT

PvG11 (+/+)

ATTATTAAACGCTGTTTTTTTCTCTTACTCCATTTGATAATGTTGCTACTGGTTGGTTGAGTTTGAAG
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PvG12 (+/+)

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PvG13 (+/–)

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CGTTTATTTTTCGGTCTTTTTCGGTTTTTCGGTTTCGTTTTTTTTCGGTCCAGTTATCGGTTCAGTTC
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PvG14 (+/+)

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PvG15 (+/+)

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PvG16 (+/+)

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PvG17 (+/+)

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AAGCTACTAAGAAAAACA

PvG18 (+/+)

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PvG19 (+/–)

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PvG20 (+/–)

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PvG21 (+/+)

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PvG22 (+/+)

CCCTAAATTTGATTCACAAAAGTAGACTATTTGAATACCCTTAAGAATGGAAGAAACATCTGACTTAT
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PvG23 (+/-)

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GTAGAATAT

PvG24 (+/-)

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CTTTG

PvG25 (+/+)

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PvG26 (+/-)

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PvG27 (+/-)

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PvG32 (+/+)

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PvG33 (+/-)

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PvG34 (+/+)

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PvG40 (+/-)

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CCTTTTTAAGTTTATTTTAAAAAAATGACTATAAGAAAAAAA

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PvG42 (+/+)

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PvG44(+/+)

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PvG45 (+/-)

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PvG48 (+/-)

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PvG49 (+/+)

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ATATCTAGT

PvG50 (+/+)

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PvG51 (+/+)

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